

## MORPHOLOGY AND PHYLOGENETIC RELATIONSHIPS OF CERTAIN PYRAMIDELLID TAXA (HETEROBRANCHIA)

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### ABSTRACT

The marine gastropod family Pyramidellidae is poorly known. Although numerous and worldwide, the anatomies of only a few species are known, and our understanding of this family's taxonomy and systematics is based almost entirely on shell characters.

Eight pyramidellid genera and 12 species were dissected, sectioned, and examined with SEM. Traditionally used gastropod characteristics are either absent (e.g., radula) or of little use (e.g., reproductive system minus the penis), because they are undiversified morphologically in the taxa examined herein. Characters of gut, mantle cavity, and penial complex proved most useful in developing an understanding of how the taxa in the present study may be defined.

Phylogenetic analysis of 13 taxa and 28 characters yielded six equally parsimonious cladograms of 67 steps and a consistency index of 68%. New systematic standards are proposed for defining (on the basis of synapomorphies) three of the four traditional pyramidellid subfamilies, the new subfamily Sayellinae, and the new genera *Houbricka* and *Petitella*.

To test the hypothesis that protoconch configuration is a reflection of developmental mode and not phylogeny, protoconch characters were eliminated from a second phylogenetic analysis. This yielded one cladogram, which when a taxon's developmental mode and host(s) are known, support the contention that protoconch shape is a result of developmental mode.

Historically shell characters, to the exclusion of soft-part anatomy, have been used to assign taxa to the various pyramidellid genera. Therefore, it might be tempting to rely more on anatomical characters and treat shell characters *a priori* as homoplasious. However, this study shows that members of the subfamily Pyramidellinae could only be distinguished by conchological characters, whereas in other taxa soft-part anatomy proved the most phylogenetically useful. The present study indicates that all characters (= total evidence) should be used in any phylogenetic analysis.

Key words: morphology, phylogeny, Pyramidellidae, synapomorphies, cladograms.

### INTRODUCTION

The Pyramidellidae Gray, 1840, are marine ectoparasitic gastropods that occur in boreal to tropical waters worldwide, and from the intertidal zone to several thousand meters. Pyramidellids feed on a variety of invertebrate hosts (Robertson, 1957; Ankel & Christensen, 1963; Robertson & Orr, 1961; Fretter & Graham, 1962; Scheltema, 1965; Boss & Merrill, 1965; Bullock & Boss, 1971; Robertson & Mau-Lastovicka, 1979; Boss, 1982). They pierce the host's tissues with a buccal stylet and remove host body fluids by the muscular action of their buccal pump (Ankel, 1949a; Fretter & Graham, 1949; Maas, 1965; Wise, 1993).

The systematic position of the Pyramidellidae has been controversial for over 130 years (Boss, 1982). This controversy, although caused in part by the lack of informa-

tion about this family, is also due to changing views about gastropod phylogeny (for a review of the current state of gastropod phylogeny and systematics, see Bieler, 1992). Traditionally, gastropods have been divided into three subclasses: Prosobranchia, Opisthobranchia, and Pulmonata, with the prosobranchs as primitive gastropods giving rise to both opisthobranchs and pulmonates. In this scheme, pyramidellids occupy an intermediary position between the prosobranchs and opisthobranchs (Boss, 1982). Because they have a spirally coiled calcareous shell into which the entire body is retractable, a foot with an operculum, a long proboscis, and an anteriorly oriented mantle cavity, most early authors placed them in the Prosobranchia, but because they also have such characteristics as a pallial kidney, subepithelial eyes on the median side of the tentacles, an ovotestis, and a heterostrophic protoconch, later au-

TABLE 1. A list of authors and the subclasses to which they assigned the Pyramidellidae.

Author	Subclass
Mörch, 1865	Opisthobranchia
Pelseneer, 1899	Prosobranchia
Thiele, 1929-35	Prosobranchia
Wenz, 1938-44	Prosobranchia
Thorson, 1946	Prosobranchia
Fretter & Graham, 1949	Opisthobranchia
Risbec, 1955	Prosobranchia
Boettger, 1955	Euthyneura*
Knight et al., 1960	Opisthobranchia
Taylor & Sohl, 1962	Opisthobranchia
Ghiselin, 1966	Opisthobranchia
Maas, 1965	Opisthobranchia
Hyman, 1967	Opisthobranchia
Golikov & Starobogatav, 1975	Prosobranchia
Thompson, 1976	Pectinibranchia
Minichev & Starobogatav, 1979	Opisthobranchia
Salvini-Plawen, 1980	Prosobranchia
Gosliner, 1981	Sinsitrobranchia
Robertson, 1985	Opisthobranchia
Haszprunar, 1985b, 1988a	Prosobranchia
Ponder & Warén, 1988	Heterobranchia
	Heterobranchia

\*Placed pyramidellids within Cephalaspidacea, with the Acteonidae giving rise to the Pyramidellidae.

thors placed them in the Opisthobranchia (Table 1). At present, many authors view the three classic subclasses as artificial, and several revisionary schemes have been proposed, although none have met broad acceptance (Brusca & Brusca, 1990). For example, in Haszprunar's (1985b) system, the Gastropoda are divided into two subclasses: the Caenogastropoda (= Prosobranchia) and the Heterobranchia (= Opisthobranchia, Pulmonata, and "allogastropods"). The Pyramidellidae are placed within the Heterobranchia, superorder Allogastropoda, which unites the Architectonicoidea, Pyramidelloidea, and the fossil Nerineoidea. Most recently, Haszprunar (1988a, 1990) and Ponder & Warén (1988) assign the pyramidellids to the order Heterostropha of the subclass Heterobranchia on the basis of several purported, but cladistically untested synapomorphies (e.g., lateral and rhinophoral nerves, giant neurons, ciliated strips, heterostrophy, sperm morphology, and chalazae). In this system, the pyramidellids are basal heterobranchs and represent an evolutionary link between the two subclasses (Gosliner, 1981; Robertson, 1985; Haszprunar, 1985a, b, c, 1988a, b, 1990; Healy, 1988a, b, 1993).

Confusion about the systematics of the pyramidellids and uncertainty about their role as ectoparasites is due, largely, to the lack of information about them. To date, the anatomical knowledge of a few species serve as the paradigm for a very large family (Ankel, 1949a, b, 1959; Fretter & Graham, 1949, 1962; Fretter, 1951; Risbec, 1955; Maas, 1963, 1965; Höisaeter, 1965; Brandt, 1968; Kristensen, 1970; Robertson, 1974, 1978, 1985; Haszprunar, 1985a, b, c, 1988a, b; Ponder, 1973, 1987; White, 1985; Wise, 1993).

The monophyly of the Pyramidellidae is supported by characters of the alimentary tract (e.g., buccal stylet) and mantle cavity (e.g., pigmented mantle organ) (Haszprunar, 1988a). However, relationships among members of the Pyramidellidae are unclear. In most classifications, the family is subdivided into four subfamilies: Cyclostremellinae Moore, 1966; Odostominae Pelseneer, 1928; Pyramidellinae Gray, 1840; and Turbonillinae Simroth, 1907 (Ponder and Warén, 1988). Nordsieck (1972) presented an alternative view. Traditionally, the assignment of taxa to a subfamily and how groups within these subfamilies have been defined has been based on shell characters (Tryon, 1886; Dall & Bartsch, 1904, 1906, 1909; Bartsch, 1909, 1917, 1955; Nomura, 1936, 1937, 1938, 1939, 1940; Laws, 1937a-d, 1938, 1939, 1940, 1941; Laseron, 1959; Nordsieck, 1972; Aartsen, 1977, 1981, 1987; Gofas et al. 1981; Linden & Eikenboom, 1992). Shell characters, however, have been shown to be convergent when snails live in similar habitats and may be unreliable indicators of phylogenetic relationships (Davis, 1979; Kool, 1993).

The objectives of this study are to develop a more comprehensive understanding of pyramidellid anatomy, add to our limited knowledge of this group's biology, and provide a phylogenetic framework upon which to build a more comprehensive classification for the family.

## MATERIAL AND METHODS

### Sample Material

Eight genera and 12 species (representing three of the four pyramidellid subfamilies) were collected alive for dissection, fixation, and histological examination (Table 2). The subfamily Cyclostremellinae was not examined because no specimens of the animals were available (i.e., only shells were available).

TABLE 2. Collection localities for taxa examined this study.

Taxa	Locality
<i>Boonea cincta</i> (Carpenter, 1864)	Palos Verdes, Los Angeles (34°12'N, 119°20'W), California
<i>Boonea seminuda</i> * (C. B. Adams 1839)	Wild Harbor (41°33'N, 70°36'W) & Bass River (41°40'N, 70°11'W), Massachusetts
<i>Odostomia babylonica</i> (C. B. Adams, 1845)	Indian Fill Key (24°54'N, 80°42'W), Florida
<i>Odostomia didyma</i> Verrill & Bush, 1900	Indian Fill Key, Florida
<i>Sayella hemphillii</i> * (Dall, 1884)	Cedar Key (29°08'N, 83°02'W), Florida
<i>Petitella crosseana</i> * (Dall, 1885)	Ft. Pierce (27°35'N, 80°19'W), Florida
<i>Pyramidella sulcata</i> (A. Adams, 1854)	Pago Bay (13°25'N, 144°48'W) & Tumon Bay (13°31'N, 144°48'W), Guam
<i>Pyramidella crenulata</i> (Holmes, 1859)	Ft. Pierce & Cedar Key, Florida
<i>Pyramidella mitralis</i> A. Adams, 1854	Pago & Tumon bays, Guam
<i>Turbonilla hemphilli</i> Bush, 1899	Ft. Pierce, Florida
<i>Houbricka incisa</i> * (Bush, 1899)	Ft. Pierce, Florida
<i>Tathrella iredalei</i> * Laseron, 1959	Fadian Hatchery (13°26'N, 144°49'W), Guam

\*Type species of genus

At the beginning of this study, it was my intention to add the number of genera examined by using available museum material. Holotypes (shells only) for each species were examined. However, museum specimens proved unusable because they had been placed in alcohol without first cracking the shell and the animal's bodies were not preserved.

Snails from Florida were collected throughout the year by one of two methods. In the first, the topmost substratum (approximately 2–4 cm) from inter- to subtidal sand and mud flats was placed in a 0.5 mm sieve, rinsed with seawater to remove silt and mud, and sorted under a dissecting microscope. The second method involved rinsing the underside of embedded rocks or coral rubble with seawater, and examining this debris under a dissecting microscope for pyramidellids. In Massachusetts (October 1991), *Boonea seminuda* were found on the slipper shell *Crepidula fornicata*. In Guam (July 1990), *Pyramidella mitralis* (*Otopleura mitralis* in previous literature) and *P. sulcata* were collected during night dives in both Tumon and Pago bays. During the day, these snails remain submerged within the sand, but at night they were easily collected as they crawled on top of the substratum. *Tathrella iredalei* was found on the shells of the various *Tridacna* spp. (giant clam) at Guam's Fadian Hatchery. *Boonea cincta* (*Chrysallida cincta* in most previous works) was found (August 1990) on the opercula of *Tequila eiseni* found inter- to subtidally on the rocks at Palos Verdes, Los Angeles County, California. Snails were kept alive in bowls of aerated seawater.

## Morphology

### Light Microscopy

#### (a) Observations of Living Animals

Living snails were observed and their habits noted. Photographs were taken with a Pentax 35 mm camera mounted on a Zeiss Tessavar dissecting microscope.

#### (b) Gross Dissection

Snails were prepared for dissection by first cracking their shells with a vise. Snails were dissected *in toto*, and structures of the alimentary tract and penial complex were excised and examined using either a compound or a dissecting microscope equipped with an ocular micrometer. Whole snails and their parts were routinely stained with toluidine blue to facilitate distinguishing the various organs and organ systems. Photographs were taken with a Polaroid camera (using type 52 Polapan Land film) mounted on a Nikon Labophot compound microscope.

#### (c) Histology

Snails were removed from their shells either by decalcification or by cracking the shell with a vise. The first method, utilizing a commercial decalcifier (Decalcifying solution, Krajian, J. T. Baker) to dissolve the shell, was used when serial sections of the entire snail were desired. Tissues were fixed in 10% formalin buffered in filtered seawater. Specimens were embedded in paraffin, sections were cut at 4–6  $\mu\text{m}$ , and stained with hematoxylin and eosin-Y (Sheehan & Hrapchak,

TABLE 3. Character-state distributions for 12 pyramidellid taxa and 28 characters.

Taxa	Characters																												
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	
OUT	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CINC	2	1	2	1	0	0	0	0	1	1	1	1	3	2	0	1	0	0	3	0	1	1	0	0	2	1	?	0	
SEMI	0	0	0	1	0	0	0	0	1	1	1	1	3	2	0	1	0	0	3	0	1	1	0	0	2	1	0	0	
JUDI	0	0	0	1	0	0	0	0	1	1	1	1	3	2	0	1	1	0	3	0	1	1	0	0	2	1	?	0	
DIDY	2	1	2	1	0	0	0	0	1	1	1	1	3	2	0	1	1	0	3	0	1	1	0	0	2	1	?	0	
SEMP	3	1	2	2	0	0	0	1	2	0	0	0	2	1	1	1	0	1	1	1	1	1	0	0	0	0	0	0	
CROS	3	1	2	2	0	0	0	1	2	0	0	0	2	1	0	0	?	0	0	1	1	1	0	0	0	1	0	0	
SUL	0	0	0	3	2	2	1	0	0	0	0	0	0	1	1	1	0	1	1	1	1	3	1	1	0	0	0	0	
CREN	0	0	0	3	1	1	1	0	0	0	0	0	0	1	1	1	0	1	1	1	1	3	1	1	0	0	0	0	
MIT	0	0	0	3	2	2	1	0	0	0	0	0	0	1	1	1	0	1	1	1	1	3	1	1	0	0	0	0	
HEMP	1	0	1	0	?	0	0	0	1	0	0	0	1	1	1	1	0	1	2	1	1	2	0	0	0	2	1	1	
INC	1	0	1	0	?	0	0	0	1	0	0	0	0	1	1	1	0	1	1	1	1	1	0	0	0	1	0	0	
IRED	1	0	1	0	?	0	0	1	2	0	1	0	1	1	1	1	0	1	1	1	1	1	0	0	1	2	1	1	

(Abbreviations: OUT = Amathinidae, CINC = *Boonea cincta*, SEMI = *Boonea seminuda*, JUDI = *Odostomia babylonia*, DIDY = *Odostomia didyma*, SEMP = *Sayella hemphillii*, CROS = *Petitella crosseana*, SUL = *Pyramidella sulcata*, CREN = *P. crenulata*, MIT = *P. mitralis*, HEMP = *Turbonilla hemphilli*, INC = *Houbrieka incisa*, IRED = *Tathrella iredalei*).

1980). Specimens were often secured within small pieces of *Cucumis sativus* (common cucumber), also fixed in 10% formalin buffered in seawater. This was done prior to embedding when the snail's orientation was particularly important. Photographs were taken with a 35 mm camera (using Kodak T-Max film 100 ASA) mounted on a Nikon Labophot compound microscope.

### Scanning Electron Microscopy

#### (a) Hard Parts

Shells and opercula were cleaned by sonication, air dried, coated with gold-palladium, and examined with either a Cambridge S-100, Selectron 250, or Hitachi S-570 scanning electron microscope operating at 4–10 KEV.

#### (b) Soft Parts

Tissue specimens were fixed in 2% glutaraldehyde buffered in 0.025 M sodium cacodylate in seawater. Postfixed tissues were thoroughly rinsed in sodium cacodylate buffered in filtered seawater. Specimens were dehydrated in a graded series of ethyl alcohol, critical point dried, and coated and examined as above.

### Phylogenetic Analysis

Twenty-eight characters were analyzed for eight genera and 12 species of pyramidellids. Characters were obtained from shell and soft-

part anatomy. At no time were characters eliminated or included on the basis of any preconceived ideas of how they might influence the outcome of the phylogenetic analyses. The distribution of the states of the characters is shown in Table 3.

The method of character analysis used to determine relationships of the taxa was phylogenetic systematics (i.e., cladistics) (Hennig, 1966; Lipscomb, 1984; Schuh & Farris, 1981; Farris, 1982, 1983). These relationships are expressed in cladograms that were constructed using the computer program Hennig86 (Farris, 1988). No *a priori* character weighting was employed. Successive weighting (Hennig86 option w xs;) was used to choose between equally parsimonious cladograms that were produced when the data set was reanalyzed without the protoconch characters. Successive weighting selects cladograms that require the fewest number of characters to have homoplasies (i.e., trees with the shortest length and fewest changing characters) (Carpenter, 1988; Lipscomb, 1993).

Characters were polarized using the out-group comparison method (Hennig, 1966; Watrous & Wheeler, 1981; Schoch, 1986). The family Amathinidae was chosen as the out-group, because it appears to be the sister group (i.e., most closely related) to the Pyramidellidae and is the only other family within the superfamily Pyramidelloidea.

Transformation series were determined (after polarization) for all multistate characters

TABLE 4. Transformation(s) for each multistate character. Italicized transformation series, although proposed initially were rejected, as they were incongruent with cladogram groupings constructed of other homologies.

Character	Transformation
1	0-1,2-3
3	0-1,2
4	0-2-1-3
5	0-1-2
6	0-1-2
9	0-1-2; <i>0-1,2</i>
13	0-3,2-1
14	0-1,2; 0-2-1
19	0-1-2-3
22	0-1,2,3; <i>0-1-2-3</i>
25	0-1-2
26	0-2-1

(Table 4) using the homology method outlined by Lipscomb (1992).

The relative quality of the phylogenetic results was judged using the consistency index (CI), a measure of the degree to which character state changes on a cladogram are minimal (Kluge & Farris, 1969), and the retention index (RI), a measure of the amount of homology hypothesized by the data set that is retained on the tree (Farris, 1989).

Autapomorphies were eliminated from all analyses. Although autapomorphies are very useful in defining terminal taxa, they provide no information about how taxa are related to each other. Moreover, by including them in the analyses the CI is superficially inflated (Farris, 1989).

Institutional abbreviations are as follows:

AMNH	American Museum of Natural History, New York, U.S.A.
ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania, U.S.A.
AMS	Australian Museum, Sydney, Australia
BMNH	The Natural History Museum, London, U.K.
CASIZ	California Academy of Sciences, San Francisco, U.S.A.
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts, U.S.A.
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A.
PM	Peabody Museum, Yale University, U.S.A.

Voucher specimens on deposit at USNM.

Superfamily Pyramidelloidea Gray, 1840  
Family PYRAMIDELLIDAE Gray, 1840

*Diagnosis:* Shell sharply lanceolate to roughly planispiral. Shell sculpture variable. Smooth, heterostrophic protoconch oriented 90–150° to teleoconch and often partially submerged within succeeding adult whorl. Shell aperture elongate-lenticular to ovate, with or without columellar folds. Operculum paucispiral, with subcentric nucleus. Alimentary tract comprised of acrembolic proboscis, buccal sac, buccal pump, esophagus (undifferentiated or divided into anterior and posterior sections), and a pair of salivary glands. Buccal sac containing piercing stylet. Simultaneously hermaphroditic. Euthyneurous nervous system highly concentrated and epiathroid.

*Remarks:* The Pyramidellidae is a large pandemic family. Depending on the author consulted, it contains 35–75 genera and 800–1000 or more species. The current taxonomy is based primarily on shell characters and is both disputatious and conjectural (Abbott, 1974; Boss, 1982).

*Discussion:* Shell: Shell shapes range from planispiral to acutely lanceolate. Pyramidellids, although generally small (average shell length 6 mm), may attain lengths of 50 mm. Shell sculpture, when present, varies and can be microscopic and/or macroscopic, with axial and spiral lines, axial ribs, and nodes. Sutures may be deep, shallow, shouldered, or crenulate. The heterostrophic protoconch is smooth and oriented 90–150° to the teleoconch. The protoconch configurations vary among genera. The shell aperture is generally elongate to ovate, with or without columellar folds, and palatal teeth may be present within the outer lip. The thin, paucispiral operculum has a subcentric nucleus. When columnar folds are present, the operculum may be notched to accommodate them.

Head-foot: Pyramidellids have a well-developed head, a pair of cephalic tentacles, and a large foot with an operculum that tapers posteriorly to either a blunt or acute apex. The epidermis of the tentacled head, mantle, and foot is lined with one layer of simple columnar or cuboidal cells. These cells have basal nuclei and are ciliated on the ventral surface of the foot, the lower antero-dorsal portion of the propodium, and the

mentum. Head-foot and mantle contain large basophilic, subepidermal gland cells. These cells discharge granulated droplets of mucus in the cytoplasm, and the droplets are discharged directly through the cell membrane into the space between the epidermal cells. This mucus coats the external surface of the mantle and head-foot. When present, the posterior pedal gland lies in a medial position just dorsal and parallel to the ventral surface of the foot. It has an invaginated layer of ciliated epithelial cells surrounding a lumen. Gland cells containing sulfated mucins that are stained dark purple by hematoxylin and eosin fill the pedal gland. The pedal gland opens on the postero-ventral surface of the foot. Snails that produce an attachment thread anchor themselves to the substratum or to their host. The pedal sinus complex, located within the lower portion of the foot consists of a series of sinuses surrounded by nucleated connective tissue. Muscle fibers radiate from the columella muscle into the head-foot and are interspersed throughout the gland cells and hemolymph sinuses.

Pyramidellid tentacles have often been described as rabbit-ear or donkey-ear in shape (Fretter & Graham, 1949), but such descriptions oversimplify their variability and complexity of the structure. Members of the Odostominae have a tentacular pad composed of a distinctive cluster of long cilia located inside and subterminal to the tentacle apices (Ponder, 1973). Fretter & Graham (1949) suggested these tentacular pads were sensory in nature and constructed of many fused cilia. Darkly pigmented eyes with a lens are subepithelial and on the median side of the tentacles. Eyes are usually round to ovate, but may be lenticular. Spacing or distance between the eyes varies among species.

The variably-shaped mentum is located just ventral to the head and extends, shelf-like, over the propodium (Fig. 11A-K shows the mentum shapes of the snails examined this study). Its function is usually locomotion. It is the first part of the crawling snail in contact with the substratum. Histologically, the mentum is indistinguishable from the foot, but it is innervated by the cerebral rather than pedal ganglia (Huber, 1987).

The mantle and its organs are similar for all pyramidellids (Fig. 1A-C). The long, wide anterior mantle (= skirt) narrows posteriorly to meet the visceral mass. Its right, anterior portion forms a short canal or siphon.

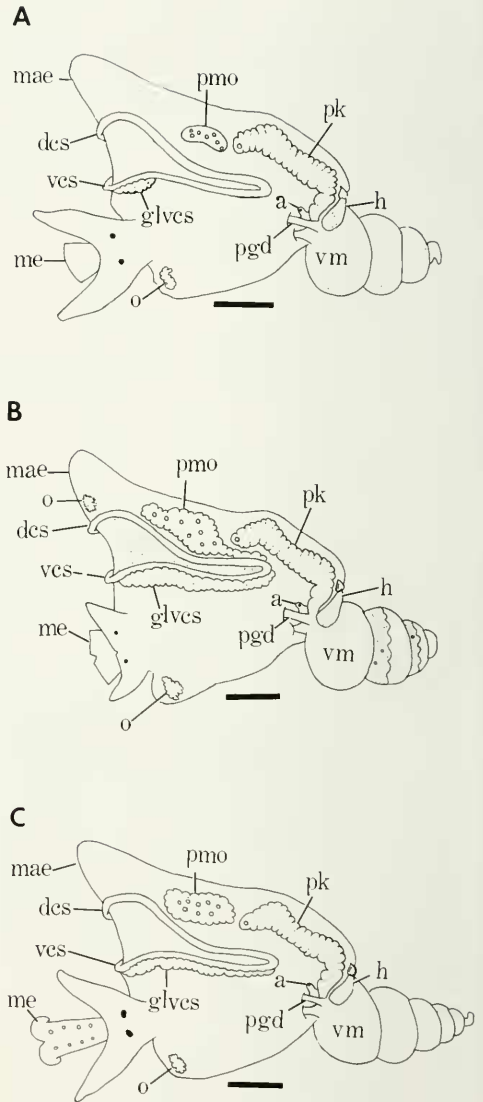


FIG. 1. Diagram of pyramidellid mantle cavities and organs: A. Subfamily Odostominae (bar = 500  $\mu$ m); B. Subfamily Pyramidellinae (bar = 1 mm); C. Subfamily Turbonillinae (bar = 500  $\mu$ m) (a = anus, dcs = dorsal ciliated strip, glvcs = gland ventral ciliated strip, h = heart, mae = mantle edge, me = mentum, o = osphradium, pgd = pallial gonoduct, pk = pallial kidney, pmo = pigmented mantle organ, vcs = visceral ciliated strip, vm = visceral mass).

**Pallial cavity:** All pyramidellids have ventral and dorsal ciliated strips (*sensu* Fretter & Graham, 1949, 1962) on the right side of the mantle cavity (Figs. 1A-C, 2A, 3A). The dorsal

strip hangs from the mantle roof immediately dorsal to the ventral strip. These strips join on the mantle roof at the posterior end of the mantle cavity. Both of these strips are constructed of a single layer of ciliated columnar cells secured to a basal lamina (Fig. 2B). The beating of the cilia is responsible for the intake and left-to-right movement of water within the mantle cavity.

A gland underlies the ventral strip (Fretter & Graham, 1962: 126). The ventral ciliated strip gland may extend the entire length of the strip (e.g., *Pyramidella*, Fig. 1B) or may underlie only 20–25% of its most anterior portion (e.g., *Odostomia* and *Boonea*, Fig. 1A). The gland is comprised of large cells filled with a viscid substance (Fig. 2C), which is sometimes released when the snail is disturbed (Table 5).

The pallial kidney is a long, tubular, narrow organ suspended from the mantle roof (Figs. 1A–C, 3A). It extends anteriorly from the heart at the visceral mass-mantle cavity junction, to immediately posterior to the pigmented mantle organ. Histologically, it consists of a series of thin-walled, slightly basophilic chambers or tubules (Fig. 3B). The papilla-like nephridiopore is located subterminally on the antero-ventral surface of the kidney (Fig. 3C, D).

A pigmented mantle organ of large, rectangular, and often multi-colored cells, is present (Figs. 3A, 4A). Genera examined have one of three shapes: (1) small and oblong (Fig. 1A), (2) large and rectangular, surrounded by a field of transparent cells (Fig. 1B), and (3) very large and elongate (with wide anterior and attenuated posterior ends), composed of many large transparent cells mixed with a few white opaque cells (Fig. 1C). In several genera, this organ produces and releases an exudate when the snail is disturbed (Table 5). Both Fretter (1951) and Ponder (1987) identified this structure as the hypobranchial gland. However, histologically and positionally, it is unlike the hypobranchial gland of other gastropods (Robertson, 1985; present study).

Only members of the Pyramidellinae have a foliobranch gill (*sensu* Robertson, 1974). This gill, first described by Risbec (1955), is composed of folds oriented perpendicular to and between the ciliated strips on the right side of the mantle roof (Fig. 4B, C). This highly folded structure ostensibly functions in gas exchange; however, it is not homologous with the gastropod ctenidium (Ponder, 1987;

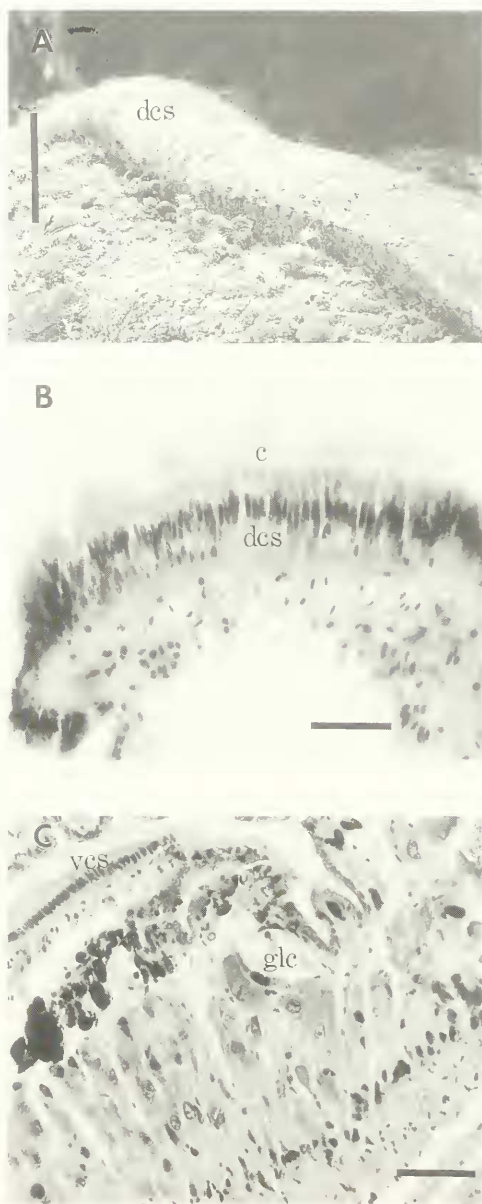


FIG. 2. A. SEM microphotograph of the ventral ciliated strip of *Pyramidella sulcata* (bar = 80  $\mu$ m); B. Longitudinal section of the ventral ciliated strip of *P. sulcata* (bar = 40  $\mu$ m); C. Longitudinal section of the gland of *Pyramidella sulcata* underlying ventral ciliated strip (bar = 200  $\mu$ m) (c = cilia, dcs = dorsal ciliated strip, glc = gland cells, vcs = ventral ciliated strip).

TABLE 5. Snail exudate origin and characteristics.

Taxa	PMO Cells	GLVCS	Exudate	Secreted by
CINC	bright yellow & a few brown orange & red	cream-colored	bright yellow	pmo
SEMI	bright yellow & a few green, clear, or brown	pink, white or light orange	bright yellow	pmo
JUDI	bright yellow & a few black, red or brown	cream-colored	bright yellow	pmo
DIDY	bright yellow, red, brown, orange, & black	cream-colored	bright yellow	pmo
SEMP	transparent & white with red, yellow & orange	darkly pigmented with a few red	milky-blue	glvcs
CROS	yellow & orange or black & white	black & white	light blue	pmo
SUL	transparent & opaque	yellow with a few red & white	light blue	glvcs
CREN	transparent & opaque	yellow with a few red & white	light blue	glvcs
MIT	opaque & clear, with a few red & yellow	yellow with a few red & white	light blue	glvcs
HEMP	clear ringed by yellow	yellow & white	yellow	glvcs & pmo
INC	clear, yellow & red	blue atop transparent matrix	bright yellow	pmo
IRED	yellow & a few white	yellow	bright yellow	glvcs & pmo

ABBREVIATIONS: CINC = *Chrysalida cincta*, SEMI = *Boonea seminuda*, JUDI = *Odostomia babylonica*, DIDY = *O. didyma*, SEMP = *Sayella hemphilli*, CROS = *Petitella crosseana*, SUL = *Pyramidella sulcata*, CREN = *P. crenulata*, MIT = *Pyramidella mitralis*, HEMP = *Turbonilla hemphilli*, INC = *Houbricka incisa*, IRED = *Tathrella iredalei*; glvcs = ventral ciliated strip, pmo = pigmented mantle organ.

Haszprunar, 1988a). Typically, the gastropod ctendium is located on the left side of the mantle cavity, has a complex series of afferent and efferent blood vessels (lacking in pyramidellids), and is composed of filaments attached to a central axis (also absent in pyramidellids).

Fretter & Graham (1949) described the location of the anus in *Odostomia* spp. and *Chrysalida* spp. as on the extreme left side at the inner most end of the mantle cavity. However, in all the taxa examined in this study (e.g., *Boonea cincta*, *Odostomia babylonica*, *O. didyma*), the rectum terminates as an anal papilla extending from beneath the common genital duct at the posterior end of the right side of the mantle floor (Figs. 1A, C, 4D). Fretter (1951), however, described the position of the anus in *Turbonilla elegantissima* and *T. jeffreysii* as in the taxa I examined.

The simple osphradium is composed of white, elliptical cells located beneath the epithelium on the extreme left side of the mantle roof. In the subfamily Pyramidellinae, part of the osphradium extends across the mantle to terminate at the right anterior corner of the mantle (Fig. 6B).

Alimentary tract: In the Odostominae, the location of the introvert-proboscis aperture is medial, on the ventral side of the head, dorsal

to the mentum base. In both the Turbonillinae and Pyramidellinae, this aperture is medial and at the anterior apex of the mentum. In the retracted condition, the introvert extends posteriorly, to pass through the nerve ring and enter the cephalic hemocoel. Although the configuration and number of alimentary structures is variable for pyramidellids, a similar ground plan is shared by all taxa (Fig. 5A): there is an acrembolic proboscis (= introvert), buccal sac (containing sucker, stylet with cuticular sheath, and stylet bulb), one or two esophagi, and a pair of salivary glands. In some genera (e.g., *Boonea* and *Odostomia*), a separate oral tube connecting the mouth and buccal pump is present (Fretter & Graham, 1949; Wise, 1993).

Reproductive system: Pyramidellids are simultaneous hermaphrodites with both ovary and testis within the lobules of the single gonad (= ovotestis). The gonad is located on the concave side of the upper visceral coils. The reproductive system is monaulic (i.e., possessing an undivided pallial gonoduct). Genera examined here have a common pallial gonoduct, extending anteriorly beneath the mantle floor to open on the right side of the head anterior to the right tentacular base above the dorsum of the foot. In some pyramidellid genera, the aperture of the common



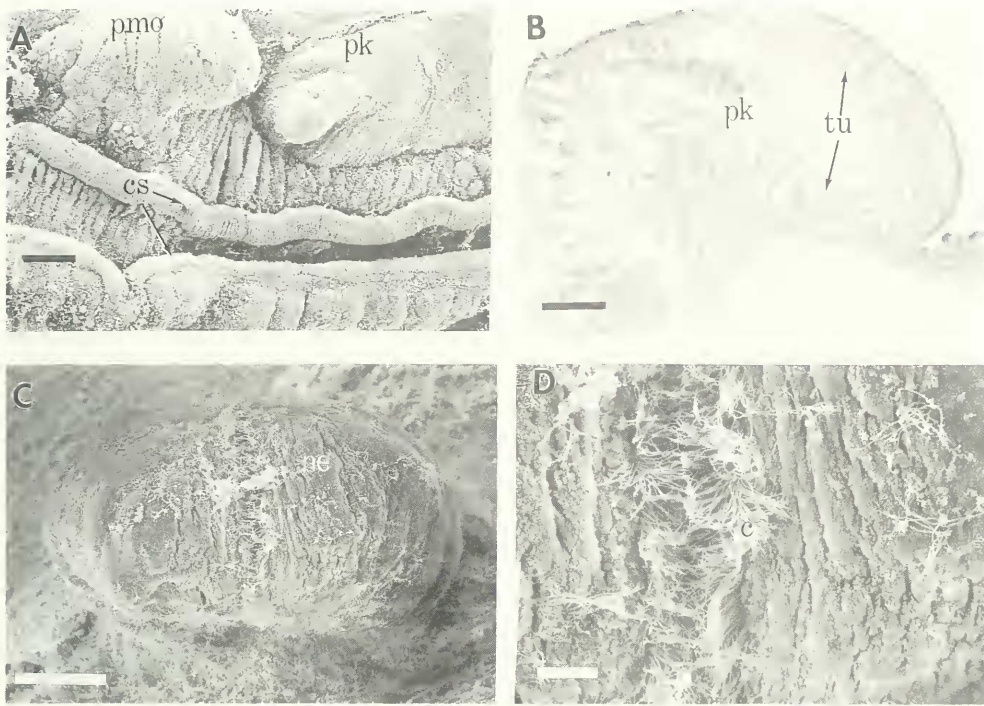


FIG. 3. A. SEM microphotograph of pigmented mantle organ, pallial kidney, and ciliated strips of *Pyramidella mitralis* (bar = 250  $\mu$ m); B. Longitudinal section of the kidney of *P. mitralis* (bar = 50  $\mu$ m); C. SEM microphotograph of anterior portion of the kidney in Fig. B. (with nephridiopore) (bar = 50  $\mu$ m); D. Enlargement of nephridial opening (bar = 10  $\mu$ m) (c = cilia, cs = ciliated strips, ne = nephridiopore, pk = pallial kidney, pmo = pigmented mantle organ, tu = tubules).

pallial gonoduct is reported to be on the mantle floor or the neck (Fretter & Graham, 1949, 1962; Robertson, 1978). Moreover, Fretter & Graham (1949, 1962) described an open, ciliated sperm groove connecting the gonoduct aperture to the penial aperture in *Odostomia unidentata*. In contrast, no ciliated sperm groove or ciliated sperm conveyance is present in any of the taxa I examined, as was determined by Robertson (1978) for *Boonea* spp. and *Fargoa* spp. Although, as suggested by Hadfield & Switzer-Dunlap (1984), in the absence of a ciliated sperm groove, a closed vas deferens should be present, no vas deferens were found in the taxa examined herein. The penis aperture is medial and immediately ventral to the mentum. Until recently (Ponder, 1987), it was believed that all pyramidellids possess a penis that lies beside the proboscis within the nerve ring (Fig. 22B, D). However, six of the eight genera examined herein have their penes within the head-foot and outside and ventral to the nerve ring (Figs. 22A, C, 12A–

C). Penis configuration is highly variable among these genera. Pyramidellids, opisthobranchs, pulmonates, and some of the superfamilies within the order Heterostropha share a modified spermatozoon that possesses a distinctive acrosome and a complex mitochondrial derivative (= paracrystalline matrix and glycogen components surrounding the axoneme) (Healy, 1988a, b, 1993).

Within the visceral mass, the ovotestis is connected to the seminal vesicle via the narrow hermaphroditic duct. A short duct connects the seminal vesicle to the coelomic gonoduct (Fig. 5B). This area of the gonoduct is the fertilization chamber and the convergence points for the seminal receptacle, albumin and mucous glands, and pallial gland (Fig. 5B) (Ponder, 1987). Fretter & Graham (1949, 1962) described two mucous glands for *Odostomia* spp. and *Chrysallida* spp. and only one for *Turbonilla elegantissima*. The proximal portion of the pallial duct (= pallial gland) appears to function in the encapsulation of the fertilized eggs prior to oviposition.

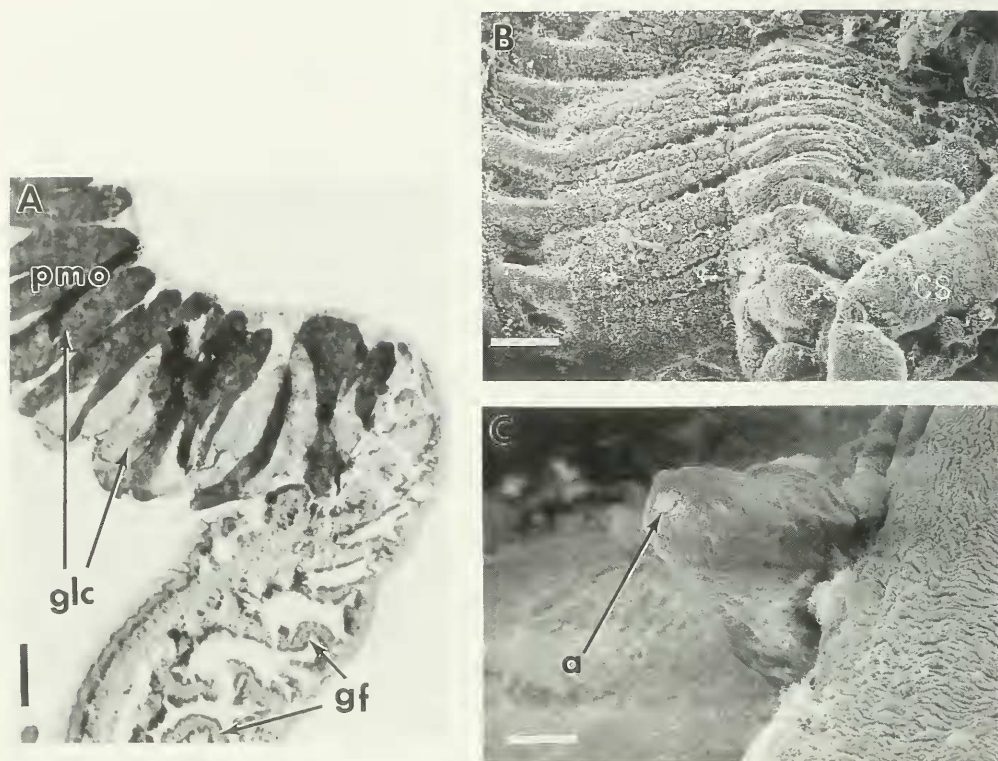


FIG. 4. A. Transverse section of the pigmented mantle organ and gill of *P. sulcata* showing cells composing the gill's filamentous folds (bar = 75  $\mu$ m); B. SEM microphotograph of the gill of *Pyramidella sulcata* (bar = 100  $\mu$ m); C. SEM microphotograph of the rectum and anal opening of *P. mitralis* (bar = 40  $\mu$ m) (a = anus, cs = ciliated strip, gf = gill fold, glc = gland cells, pmo = pigmented mantle organ).

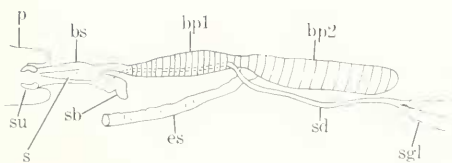
The anterior, distal portion of the pallial gonoduct may function as a prostate (Fretter & Graham, 1949, 1962).

Nervous system: (Fig. 6A) In pyramidellids, the nervous system (minus the osphradial ganglion) is comprised of a highly concentrated ring within the head that encircles the alimentary tract and, in some genera, the penis (Fretter & Graham, 1949; Huber, 1987; this study). The nervous system is further described as being epiathroid, because the pleural ganglia lie adjacent to cerebral ganglia (Haszprunar, 1988a). The outlying osphradial ganglion is connected to the supraesophageal by a long nerve extending across the nerve ring immediately anterior to the proboscis. In the Pyramidellinae, the portion of the osphradium that extends across to the right side of the mantle is innervated by a nerve arising from the osphradial nerve, located approximately one-half the distance to the osphradial ganglion (Fig. 6B). The pres-

ence of the osphradium and its ganglion on the snail's left side suggests its euthyneurous condition (= untwisted visceral loop) is a result of concentration of the nerve ring and not detorsion (Fretter & Graham, 1949; Haszprunar, 1985c, 1988a).

The arrangement of the nervous system for the taxa examined in the present study is as described by Fretter & Graham (1949) and Huber (1987, 1993), with some exceptions: (1) Members of the subfamily Pyramidellinae examined here have a nerve extending from the osphradial nerve (originating at the supraesophageal ganglion) to innervate a portion of the osphradium that extends to the right anterior mantle corner just posterior of the mantle edge (Fig. 6B); (2) labial ganglia described by Fretter & Graham (1949) for constituents of the Odostominae, were not apparent in any of the taxa examined this study; (3) the subesophageal ganglion has been depicted as spheroid and identical to

A



B

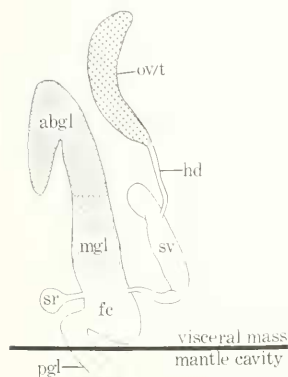
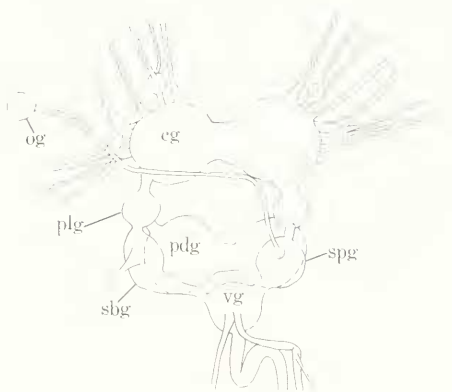


FIG. 5. A. Diagram of generalized pyramidellid feeding structures; B. Diagram of generalized pyramidellid reproductive system (abgl = albumin gland, bp1 = buccal pump 1, bp2 = buccal pump 2, bs = buccal sac, es = esophagus, fc = fertilization chamber, hd = hermaphroditic duct, mgf = mucous gland, ov/t = ovotestis, p = proboscis, pgl = pallial gland, sd = salivary gland duct, sgl = salivary gland, sr = seminal receptacle, s = stylet, su = sucker, sv = seminal vesicle).

the supraesophageal ganglion (Fretter & Graham, 1949; Haszprunar, 1988a, 1990). In all of the taxa examined in this study, the esophageal ganglia are asymmetrical, with the subesophageal ganglion being oblong and the supraesophageal spheroid (Fig. 6A); (4) the osphradial nerve, as it extends to the osphradium from the supraesophageal ganglion, passes beside and anterior to the proboscis and not posterior to the proboscis (Fretter & Graham, 1949; Haszprunar 1988a) (Fig. 6A); and (5) the rhinophoral and lateral nerves, described by Huber (1987, 1993) for various pyramidellids, and used by Haszprunar (1988a, 1990) to hypothesize that the Pyramidellidae are sister taxa to the opisthobranchs, are not homologous with those nerves of the same name in the opisthobranchs described by Huber (1987, 1993). In some opisthobranchs (e.g., Architectibranchia),

A



B

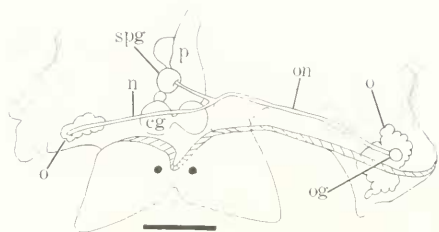


FIG. 6. A. Diagram of generalized pyramidellid nervous system. Buccal ganglia not illustrated; B. Diagram of the nervous system of *Pyramidella* sp. showing the nerve that splits from the main osphradial nerve to innervate that portion of osphradium located on the left side of the mantle (bar = 1 mm) (cg = cerebral ganglia, n = nerve, o = osphradium, og = osphradial ganglion, on = osphradial nerve, pdg = pedal ganglia, plg = pleural ganglia, sbg = subesophageal ganglion, spg = supraesophageal ganglion, vg = visceral ganglion).

the rhinophoral nerves innervate the posterior portion of the Hancock's organ, whereas in others (e.g., Aplysiomorpha and Bullomorpha) these nerves innervate the rhinophores. These structures are not considered to be homologous (pers. comm., Gosliner, 1992). Moreover, all known pyramidellids do not possess either a Hancock's organ or rhinophores (the nerves Huber [1987] identified as rhinophoral in the pyramidellids he examined, innervate the lateral walls of the head—an area he suggested probably contains sensory cells). Huber (1987) stated that the lateral nerves, which originate on the pedal ganglia near the pleuro-pedal connective, occur in pyramidel-

lids, opisthobranchs, and pulmonates. In the Architectibranchia, these nerves innervate the lateral body walls, as well as parts of the columella muscle, whereas in Aplysiomorpha and Bullomorpha, Huber only listed them as present. In primitive pulmonates (e.g., Archaeopulmonata), the lateral nerves innervate portions of the pharynx, while in pyramidellids, he determined they innervate the muscles of the lateral body wall. As with the rhinophoral nerves, it is not possible to consider the lateral nerve homologous across the taxa he examined. Moreover, examination of just the opisthobranchs (illustrated by Huber, 1987) revealed that the rhinophoral and lateral nerves are interchangeable, and therefore fail the positional test of homology as defined by Remané (1955).

**Life history:** The literature contains a limited amount of life-history data (Lebour, 1932; Thorson, 1946, 1950; Ramussen, 1944, 1951; Amio, 1963; Robertson, 1967, White, 1985). Pyramidellids for which longevity is known have a life span of one year (Rasmussen, 1944; Wells, 1959; Nishino et al. 1983; White et al., 1985; McFadden & Myers, 1989; pers. obser.). The spawning season for snails living in temperate to subtropical regions is generally 3–4 months. Cumming (1988, 1993) discusses the spawning behavior of a single tropical species in a mariculture setting. Pyramidellids deposit their eggs in a continuous string called a chalazae. The chalazae is composed of eggs joined end to end by threads that are continuous with the wall of the cocoon. These strings are molded into a gelatinous egg mass.

#### Character Descriptions

#### SHELL CHARACTERS

##### (1) Protoconch angle

- 0—120–125° (Figs. 9C, 19F)
- 1—90–95° (Fig. 25C)
- 2—130–135° (Fig. 14C)
- 3—140–145° (Fig. 15D)

**Remarks:** The protoconch is the larval shell formed prior to metamorphosis into the juvenile stage. The protoconch angle is the angle at which the protoconch axis is oriented to the axis of the adult shell.

##### (2) Orientation of protoconch

- 0—sinistrally heterostrophic (Figs. 9C, 25C, 29D, & 24H)

- 1—dextrally heterostrophic (Figs. 7C, 14C, 15D, & 18D)

**Remarks:** In state 0, the protoconch generally lies across the teleoconch, with its earliest portion partially submerged (Fig. 9C) or completely exposed (Fig. 25C). In state 1, the earliest portion of the protoconch is completely submerged within the teleoconch and coils upwards. The terms sinistrally and dextrally heterostrophic are adopted from Fretter et al. 1986 (p. 557, fig. 377) and are used here to describe the relationship of the protoconch to the teleoconch.

##### (3) Number of protoconch whorls

- 0—2.0 (Fig. 23E)
- 1—2.5–3.0 (Fig. 28C)
- 2—1.0–1.5 (Fig. 18D)

**Remarks:** The number of protoconch whorls were determined using the method outlined by Robertson (1976).

##### (4) Columellar fold

- 0—absent—No apparent columella fold(s) at aperture (Fig. 29B)
- 1—a single, prominent and acute fold on the upper one-half of the columella perpendicular to the columella axis (Fig. 9B)
- 2—a single, less acute fold, which begins basally on the columella to extend, at an oblique angle to the upper half of the columella (Fig. 15C)
- 3—one large fold on the upper half of the columella dorsal to two smaller folds, all three perpendicular to the columella (Fig. 19C)

**Remarks:** The columella is the solid or hollow pillar formed by the adaxial walls of the whorls and surrounds the axis of the coiled shell (Knight et al., 1960). The columellar fold is a spirally wound ridge on the columella that is readily seen at the shell's aperture. Slight swellings on the columella deep within the body whorl and, therefore, not visible at the aperture were not considered to be homologous to columellar folds in this study (e.g., as in *Tathrella iredalei*) (Fig. 29F).

In the outgroup, Amathinidae, genera with limpet-like shells (e.g., *Amathina*) lack a columella. Other genera (e.g., *Clathrella*) have a littoriniform shell with a columella. Only the latter genera were used to polarize characters of the columella.

## (5) Columellar fold ridges

- 0—columellar smooth or unridged (9B, 15C)
- 1—a single ridge with non-overlapping or imbricate plates (23D)
- 2—2–4 ridges of many imbricate plates (19D&E).

## (6) Palatal teeth

- 0—absent
- 1—3 to 4 (Fig. 23C)
- 2—6 to 8 (Fig. 19C)

*Remarks:* Fully formed palatal teeth, or folds, are located deep inside the outer lip of the shell's aperture. Because the palatals located immediately inside the aperture are undeveloped and depend on the age of the snail, they were not used as characters.

## Operculum Character

## (7) Operculum notched to accommodate columellar fold.

- 0—absent (Figs. 13F, 28F)
- 1—present (Fig. 19I)

*Remarks:* All genera examined herein possess an operculum composed of a brown, hardened, and proteinaceous substance. Only taxa of the subfamily Pyramidellinae have an operculum that is notched to accommodate the largest columellar fold.

## External Anatomy Characters

## (8) Tentacles

- 0—connate (Figs. 21A–C, 8A–D)
- 1—not connate (Figs. 21D, 17A, B)

*Remarks:* Connate tentacles are joined along their anterior base.

## (9) Tentacle shape

- 0—triangular and laterally folded (Fig. 21A)
- 1—subtriangular and ventro-laterally folded (Figs. 8A, D, 21B, C)
- 2—cylindrical (Figs. 21D, 17A, B)

## (10) Tentacular pads

- 0—absent
- 1—present

*Remarks:* Tentacular pads are composed of fused cilia that are located subterminally, at the apex of the tentacles. These pads are only

found in members of the subfamily Odostominae.

## (11) Attachment thread

- 0—absent
- 1—present.

*Remarks:* Attachment threads may be produced by the pedal gland to secure the snail to the substratum or its host. Pedal threads are absent in taxa that are infaunal.

## (12) Bifurcate mentum

- 0—present (Fig. 11D–I)
- 1—absent (Fig. 11A–C)

*Remarks:* The mentum is a shelf-like projection immediately dorsal to the propodium. The mentum, in all but one of genera examined in this study, extends beyond the foot to the substratum when the snail is moving. Its shape is highly variable among examined genera.

## (13) Anterior mentum edge

- 0—incised (Fig. 11D, F)
- 1—retuse (Fig. 11E, G)
- 2—emarginate (Fig. 11H, I)
- 3—unnotched (Fig. 11A–C)

## Alimentary Tract Characters

## (14) Introvert-proboscis aperture

- 0—on the dorsal surface of the mentum base
- 1—medial on the mentum tip
- 2—ventral side of the head dorsal to the mentum

*Remarks:* This aperture is the opening through which the acrembolic (= completely invaginable) proboscis passes upon protraction or retraction.

## (15) Four-way junction

- 0—absent (Figs. 8A–D, 17B)
- 1—present (Figs. 21A–D, 17A)

*Remarks:* The four-way junction is formed by the convergence of the anterior esophagus, posterior esophagus, and paired salivary glands.

## (16) Buccal pump

- 0—buccal pump without blind sac or caecum (Fig. 17B)
- 1—with blind sac (Figs. 8A–D, 17A, 21A–D)

*Remarks:* The buccal pump is that portion of the gut between the buccal sac and esophagus.

(17) Distal portion of buccal pump (= bp2)

- 0—laterally flattened (8A, 17A, 21A)
- 1—circular (8C)

*Remarks:* Descriptions refer to shape of distal end of buccal pump when viewed in cross-section.

(18) Buccal pump

- 0—outside the proboscis sheath
- 1—within the proboscis sheath

*Remarks:* When the proboscis is retracted the buccal pump may lie within or outside of the proboscis sheath.

(19) Salivary gland ducts

- 0—not within or attached to buccal pump or esophagus (Fig. 17B)
- 1—attached to the exterior of anterior esophagus (Figs. 17A, 21A,C, D)
- 2—within the walls of anterior esophagus (Fig. 21B)
- 3—within the walls of buccal pump (Fig. 8A–D)

*Remarks:* The ducts of the salivary glands extend anteriorly to penetrate the stylet bulb, where they unite to form a single duct entering the stylet.

(20) Salivary gland terminus

- 0—attachment absent (Fig. 8A–D)
- 1—attachment present (Figs. 17A–B, 21A–D)

*Remarks:* The salivary glands are elongate, slender organs composed of few to numerous cells bordering a central ciliated lumen. The posterior end of each gland terminates in a vesicle-like bladder that can be attached to the posterior esophagus by a fine thread of muscle or connective tissue.

(21) Buccal stylet

- 0—absent
- 1—present

*Remarks:* The stylet, purportedly made of chitin, is enclosed within a sheath.

Pallial Cavity Characters

(22) Pigmented mantle organ

- 0—absent
- 1—small, oblong and anterior of the kidney (Fig. 1A)
- 2—large, rectangular and oblong mass comprised of pigmented cells surrounded by transparent cells just anterior of the kidney (Fig. 1C)
- 3—very large, wide anterior with attenuated posterior that extends to the juncture of the dorsal and ventral ciliated strips (Fig. 1B)

*Remarks:* The pigmented mantle organ which hangs from the mantle roof just to the right of center, produces an opaque to colorful, viscous substance that is released when the snail is disturbed (Table 5).

(23) Secondary gill

- 0—absent
- 1—present

*Remarks:* When present, the gill is located between the opposing ciliated strips (Fig. 4B). The outgroup has a "gill" to the right of the dorsal ciliated strip and is not homologous to the pyramidellid gill. It is in a different position in the mantle cavity and is comprised of thin sheets or leaves, in contrast to fairly thick ridges as in the pyramidellids. Moreover, neither is homologous with the gastropod ctenidium, on the basis of position, blood supply, and structure.

(24) Osphradium

- 0—subtriangular, left side only
- 1—subtriangular on the left side and extends across mantle to right mantle corner, just inside mantle edge

(25) The gland beneath the ventral ciliated strip

- 0—underlies entire ventral ciliated strip (Fig. 1B)
- 1—underlies 50–60% of the strip (beginning anteriorly and extending posteriorly)
- 2—underlies only 20–25% of the anterior portion of strip (beginning anteriorly and extending posteriorly) (Fig. 1A)

(26) Exudate

- 0—secreted from the ventral ciliated strip gland
- 1—secreted from the pigmented mantle organ

- 2—secreted from both the ventral ciliated strip gland and the pigmented mantle organ

*Remarks:* A viscid exudate is secreted when the snail is disturbed (Table 5). The exudate is believed to be repugnant to repel potential predators (Robertson, 1985; pers. obser.)

#### Penial Characters

##### (27) Penis position

- 0—outside the nerve ring (Figs. 22A, C, 12A–C)  
1—a portion of the penis lies within the nerve ring (Figs. 22B, D)

##### (28) Penial sperm sac

- 0—absent  
1—present (Figs. 22B, D)

#### Phylogenetic Analysis

Classical evolutionary taxonomic schemes use conchological characters to subdivide the Pyramidellidae into four subfamilies (Abbott, 1974; Boss, 1982). This study is the first to use cladistic (= phylogenetic) methodology to test the validity of three of the subfamilies and to construct hypotheses about the relationships of the species. The following results and discussion are presented in two parts. The first focuses on the relationships of the taxa as indicated by the cladograms, and briefly, the taxonomic implications of these relationships. The second examines conflicting hypotheses of relationships when soft-part anatomy and protoconch characters are considered separately. To aid in the discussion of the cladograms, clades are labelled as units I–IV (Figs. 30–35).

#### Relationships within the Pyramidellidae

Six equally parsimonious cladograms (Figs. 30–35) are produced using the data set of 28 characters and 13 taxa (Table 3). All trees have a length of 67 steps, a consistency index (CI) of 68, and a retention index (RI) of 81. Final transformation series for multistate characters are listed in Table 4.

A clade uniting *Odostomia babylonica*, *O. didyma*, *Boonea seminuda*, *B. cincta* is found (unit I in Figs. 30–35) in all trees. *Boonea cincta* has previously been placed in the genus *Odostomia*, subgenus *Chrysallida*. This clade corresponds to the subfamily Odostominae. In traditional classifications (Dall & Bartsch, 1904; 1909), taxa were assigned to the Odostominae if their shells were short,

subconic or ovate in shape, unsculptured or cancellate, possessed few whorls, and had a single columellar fold. Here I propose that the Odostominae (represented by the taxa in unit I; Figs. 30–35) are monophyletic and that their definition be expanded by seven synapomorphies: columellar fold (state 4–1), tentacular pads (state 10–1), mentum not bifurcated (state 12–1), shape of anterior mentum edge (state 13–3), introvert aperture location (state 14–2), position of salivary gland ducts within the alimentary tract (state 19–3), and the size of the gland beneath ventral ciliated strip (state 25–2). Also defining this clade are two convergent character states: tentacle shape (state 9–1) and pedal thread (state 11–1).

Within unit I, relationships among *O. babylonica*, *B. seminuda*, and the *O. didyma/B. cincta* sister group, while resolved in Figures 30, 32, and 34, are unresolved in Figures 31, 33, and 35. In all cladograms (Figs. 30–35), *Boonea cincta* and *Odostomia didyma* are shown to be more closely related to each other than either is to *B. seminuda* and *O. babylonica*. In these trees then, the genus *Odostomia* is not monophyletic. This apparent paraphyly is dependent upon protoconch character states 1–3 that group *B. cincta* and *O. didyma*. This sister taxa grouping is contrary to characters of soft-part anatomy, which indicate that *O. babylonica* and *O. didyma* are most closely related. Moreover, on the basis of soft-part anatomy (particularly due to similarities of the alimentary tract) *Boonea cincta* and *B. seminuda* are sister taxa. Consequently, *Chrysallida cincta* Carpenter is transferred to the genus *Boonea*.

In all cladograms (Figs. 30–35), units II–IV (sister taxa to the Odostominae [unit I]) form a monophyletic group on the basis of five character states. These synapomorphies include: introvert-proboscis aperture medial on mentum tip (state 14–1), portions of the alimentary tract forming a four-way junction (state 15–1), buccal pump within the proboscis sheath (state 18–1), salivary gland ducts attached to the exterior of the anterior esophagus (state 19–1), and the salivary gland's terminal end attached to the posterior esophagus by a fine thread (state 20–1).

Unit II, composed of *Sayella hemphillii* and *Petitella crosseana* (formerly placed in *Sayella*) are united as sister taxa in all cladograms (Figs. 30–35) because they share two synapomorphies: protoconch angle (state 1–3) and columellar fold configuration (state 4–2) and four convergences: dextral hyperstrophy (state 2–1), number of protoconch

whorls (state 3–2), tentacles not connate (state 8–1) and tentacle shape (state 9–2). These characters are, however, in conflict with characters (15–19) of the alimentary tract. Although grossly their respective head and foot are similar, these two species are anatomically very different. Furthermore, when protoconch character (state 3–1) is eliminated from the phylogenetic analysis, these taxa are no longer united and their close kinship no longer supported (Fig. 36).

This study shows that *Sayella hemphilli* and *Petitella crosseana*, both originally assigned to the same genus, and to the Odostominae solely on the basis of overall shell shape and the number of columellar folds, do not belong in the same genus nor should either be considered any longer a member of this subfamily. *Sayella hemphilli* is anatomically very different from all described odostomian species, and the anatomy of *P. crosseana* is unlike any described pyramidellid. Consequently, *Sayella crosseana* is assigned to the new genus *Petitella*, and both taxa are placed in the new subfamily Sayellinae because they are distinct from our current constructs of existing pyramidellid subfamilies as shown here.

The clade composed of *Pyramidella sulcata*, *P. crenulata*, and *P. mitralis* (unit III; figures 30–35) is equal to the subfamily Pyramidellinae. Originally, pyramidellids were allotted to this subfamily if their shell shape was elongate-conic, the shell surface was polished, the adult whorls were flat-sided and the columella had 1–3 columellar folds (Dall & Bartsch, 1904, 1909). As stated above, shell characters of this nature may provide confusing and poorly defined guidelines for assigning taxa to phylogenetically meaningful groups. Here the monophyly of the Pyramidellinae is proposed on the basis of five synapomorphies: presence of three columnar folds (state 4–3), notched operculum (state 7–1), size and shape of pigmented mantle organ (state 22–3), presence of a secondary gill (state 23–1), and the configuration of the osphradium (state 24–1) (Figs. 30–35). Within unit III, *Pyramidella mitralis* and *P. sulcata* are sister taxa relative to *P. crenulata*, because they share the same number of columellar fold ridges (state 5–2) and shell apertural palatal teeth (state 6–2). Paradoxically, the members of this clade cannot be distinguished from one another on the basis of the soft-part anatomy examined in this study. *Pyramidella sulcata* can only be separated from *P. mitralis* by over-

all shell shape (Figs. 14, 19) and minute perforations of the shell (Fig. 19A). Shell characters also separate *Pyramidella crenulata* from *P. sulcata*; the former is much smaller, and its sutures are crenulated (Fig. 18B). These shell characters, because they are autapomorphies, were not included in the analysis.

Taxa of the subfamily Pyramidellinae (unit III), as discussed above, are only separated into species on the basis of shell characters. Anatomically these taxa are nearly identical.

*Turbonilla hemphilli*, *Houbricka incisa* (formerly *Turbonilla incisa*), and *Tathrella iredalei* are united in a clade (unit IV; Figures 30–35) that, at least in part, corresponds to the subfamily Turbonillinae. Pyramidellids were assigned to the subfamily Turbonillinae if their shell shape was lanceolate, their adult whorls were numerous and the whorls had pronounced axial ribs (Dall & Bartsch, 1904, 1909). Here the monophyly of the Turbonillinae is proposed and supported by four synapomorphies: incised anterior mentum edge (state 13–1), exudate origin (state 26–2), position of the penis through the nerve ring (state 27–1), and presence of a sperm sac (state 28–1).

In all trees (unit IV) (Figs. 30–35), *Houbricka incisa* is separated from the *Turbonilla hemphilli*/*Tathrella iredalei* sister group on the basis of several anatomical differences: anterior mentum edge (state 13–0), pigmented mantle organ shape (state 22–1), origin of repugnatory exudate (state 26–0), and penial complex (states 27–0 and 28–0). Therefore, the genus *Turbonilla* is paraphyletic in all trees (Figs. 30–35). Prior to this study, the anatomy of both species was unknown, and both were included in the same genus because of their lanceolate shell and protoconch configuration. *Houbricka incisa* is anatomically very different from *Turbonilla hemphilli* or any of the other taxa currently assigned to this genus. Therefore, the new genus *Houbricka*, with *Turbonilla incisa* Bush as the type species, is proposed herein. *Tathrella iredalei* is provisionally retained in the subfamily Turbonillinae because it possesses synapomorphies that seem to justify this placement.

#### Protoconch Characters vs. Anatomical Characters

Members of the Pyramidellidae are generally only known from their shells (Abbott, 1974; Fretter et al. 1986, Haszprunar, 1988a). Moreover, the lack of understanding of this family's biology and anatomy is often attrib-



uted to the difficulty associated with studying such small snails (Haszprunar, 1988b). Consequently, with a better understanding of their anatomy, it is not surprising that oversplit taxonomic groupings based on shell characters alone may be in conflict (= incongruent) with anatomical characters. When the protoconch characters 1–3 are suppressed (Hennig86 option cc);, 20 equally parsimonious cladograms are produced. After successive weighting (Hennig86 option xs w.);, one tree remains with a length of 57 steps, a CI of 81, and a RI of 90. In this cladogram both *O. didyma*/*O. babylonica* and *B. seminuda*/*B. cincta* are sister taxa (Fig. 36). Contrary to the relationships suggested by the protoconch characters, feeding structures suggest that *O. babylonica* and *O. didyma* are most closely related (= sister taxa). They essentially share the same gut configuration, the only difference is that the salivary gland ducts in *O. babylonica* exit the gut just prior to the stylet bulb (Fig. 8C). *Boonea seminuda* and *B. cincta* share the same gut configuration and differ only in the length of buccal pump one (bp1). The bp1 of *B. cincta* is equal to the length of the buccal pump two (bp2), whereas in *B. seminuda* the bp1 is 1.5 times the bp2 (Fig. 8B).

These conflicting hypotheses of relationships may be explained by the fact that protoconch shape is a reflection of developmental mode and not phylogeny. Historically, protoconch configuration has been correlated with the type of larval development rather than phylogeny (Reid, 1989). For constituents of the Odostominae in the present study, our knowledge of larval development is limited to *B. cincta* and *B. seminuda*. *Boonea cincta* undergoes direct development (i.e., non-planktonic) and recently metamorphosed individuals crawl away from the egg mass within 25 to 28 days (LaFollette 1979). *Boonea seminuda* is lecithotrophic and in the plankton for approximately two weeks (Robertson, 1978). Species with non-planktotropic development and no planktonic stage typically may have a large smooth protoconch (i.e., highly inflated) of few whorls and generally are not distinguishable from the adult shell. *Boonea cincta* meets two of the three criteria; however, its smooth protoconch is easily delimited from the highly sculptured adult shell (Fig. 7C). Generally, snails that are lecithotrophic have a protoconch of a few whorls of intermediate size (i.e., less inflated). This condition is present in *B. seminuda* (Fig. 9C–E). Therefore, developmental modes are different in

these two species, as are their respective protoconch shapes. The protoconch characters are incongruent with the other characters and rejected as synapomorphies. What of *O. babylonica* and *O. didyma*? Their protoconch shapes are very different. Is this, too, a reflection of developmental mode and not phylogeny? The only way to determine this is to discover their developmental modes, which when treated as characters, can be mapped onto a cladogram of the working phylogeny for the group and checked for congruence with other characters.

What of convergences in gut or feeding-structure anatomy as a result of feeding on similar hosts? The hosts for both *B. seminuda* and *B. cincta* are known. *Boonea seminuda* parasitizes a number of hosts across its range (e.g., *Crepidula fornicata* and *Aequipecten qibbus*), whereas *B. cincta* feeds on a number of trochiid gastropods (e.g., *Norrisia norrisi*) and *Haliotis* spp. These hosts are all different, indicating that feeding structure anatomy is a reflection of phylogeny and not adaptation. The hosts for *O. babylonica* and *O. didyma* are not known.

Protoconch and adult shell characters (e.g., similar columellar fold configurations) also united *S. hemphillii* and *Petitella crosseana* as sister taxa in the initial cladograms, whereas anatomical characters separate the two (Fig. 36). Although they both have a grossly similar head-foot (e.g., tentacles not connate, tentacles cylindrical, similar shaped and emarginate mentum, and location of introvert opening—none of these are unique to the two), they are very dissimilar anatomically. They have very different alimentary tract (Fig. 17A, B) and penial configurations (Fig. 12A, B). The paraphyly of the genus *Turbonilla*, as depicted in Figures 30–35, is even more apparent when the protoconch characters were eliminated from the phylogenetic analysis (Fig. 36). However, until both developmental modes and hosts are known for these species, it is impossible to eliminate the protoconch characters as completely phylogenetically uninformative and/or choose between competing hypotheses of relatedness (i.e., between phylogeny and convergent adaptation).

Historically, shell characters, to the exclusion of soft-part anatomy, have been used to assign taxa to the various pyramidellid genera. Consequently, it might be tempting to rely more on anatomical characters and treat conchological characters *a priori* as homoplastic and uninformative. However, as stated above,

I was only able to distinguish members of the subfamily Pyramidellinae on the basis of shell morphology, whereas in other taxa, soft-part anatomy proved most informative in determining relatedness. Therefore, the present study indicates that all characters (= total ev-

idence, *sensu* Jones et al., 1993) should be used in a phylogenetic analysis. In addition, it is only by testing these characters for congruence with other characters, that the often complex relationships between taxa can be resolved.

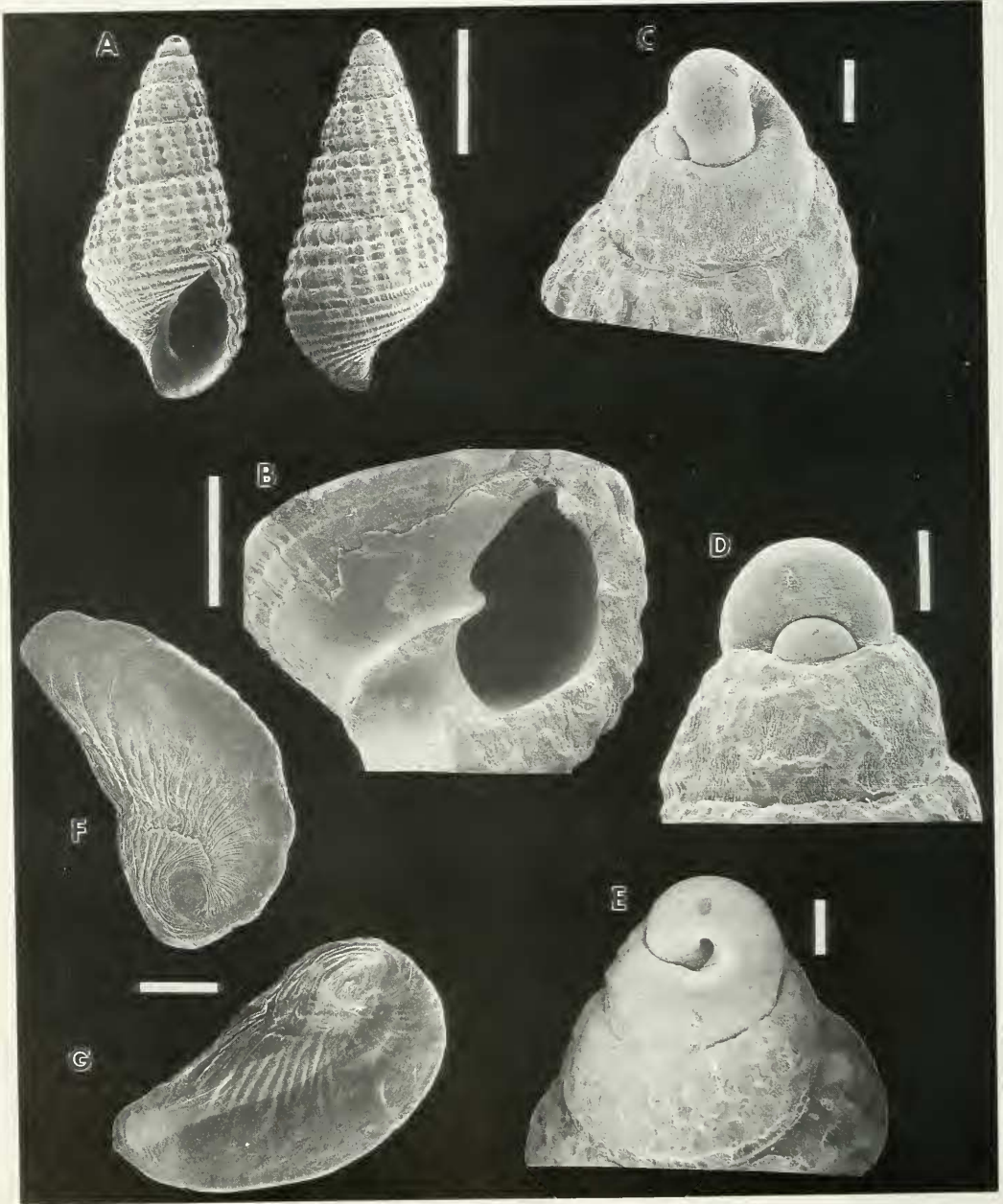


FIG. 7. Shell morphology of *Boonea seminuda*. SEM microphotographs: A. Apertural and dorsal views of shell (bar = 1 mm); B. Aperture and columellar fold (bar = 400  $\mu$ m); C. Tilted, frontal view of protoconch (bar = 100  $\mu$ m); D. Lateral view of protoconch (bar = 100  $\mu$ m); E. Tilted, lateral view of protoconch (bar = 100  $\mu$ m); F. Unattached surface of operculum; G. Attached surface of operculum (bar = 200  $\mu$ m).

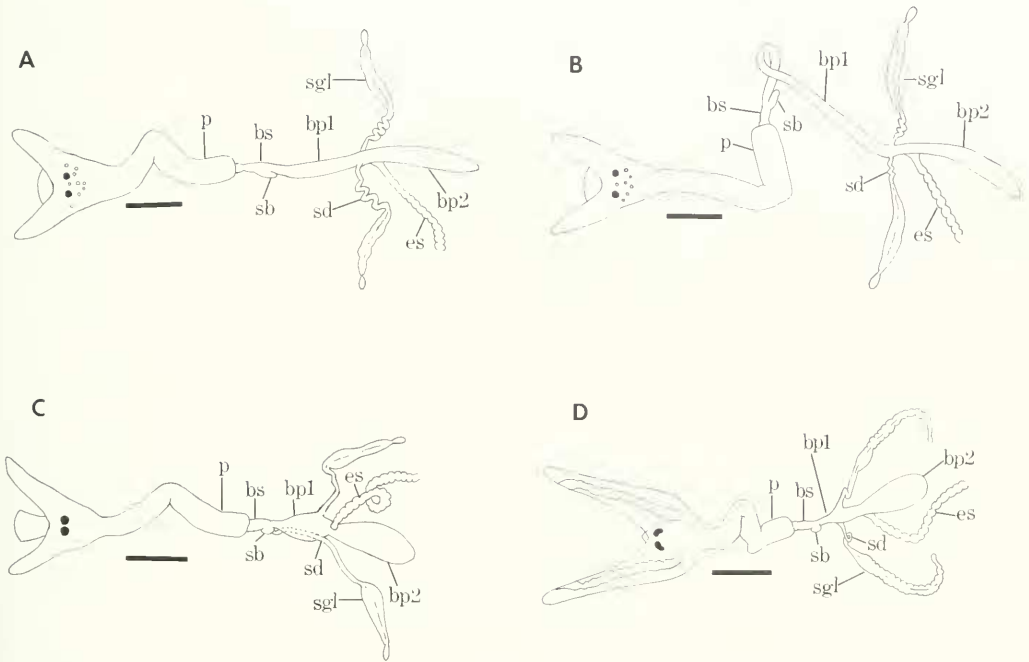


FIG. 8. Diagram of pyramidellid alimentary tracts. A. *Boonea cincta* (bar = 200  $\mu$ m); B. *Boonea seminuda* (bar = 500  $\mu$ m); C. *Odostomia babylonica* (bar = 150  $\mu$ m); D. *O. didyma* (bar = 150  $\mu$ m). (bp1 = buccal pump 1, bp2 = buccal pump 2, bs = buccal sac, es = esophagus, p = proboscis, sb = stylet bulb, sd = salivary gland duct, sgl = salivary gland, su = sucker).

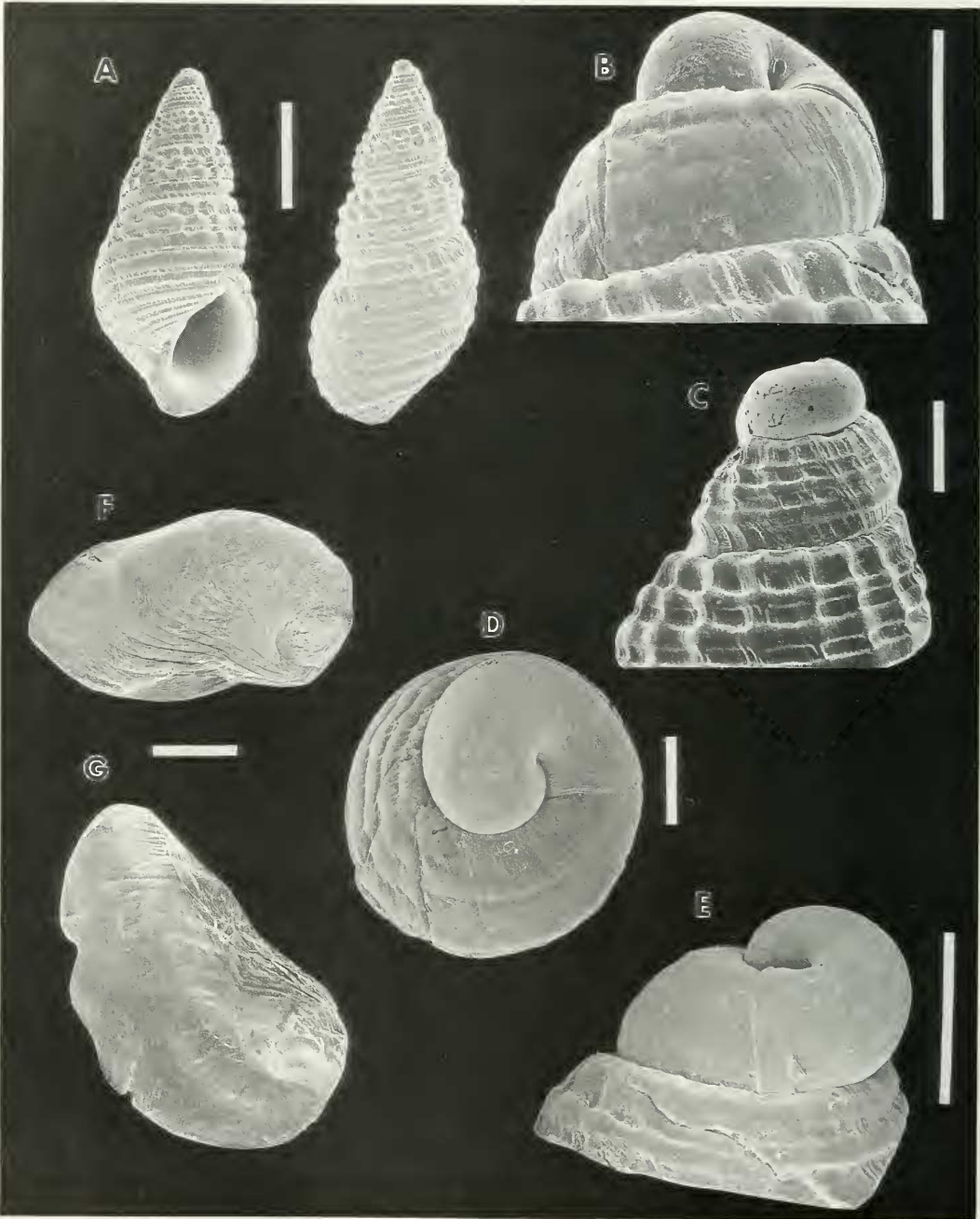


FIG. 9. Shell morphology of *Boonea cincta*. SEM microphotographs: A. Apertural and dorsal views of shell (bar = 1  $\mu$ m); B. Frontal view of protoconch (bar = 100  $\mu$ m); C. Lateral view of protoconch and first two adult whorls (note smooth protoconch vs. cross-hatched teleoconch) (bar = 200  $\mu$ m); D. Apical view of protoconch showing demarcation of larval and adult shells (bar = 150  $\mu$ m); E. Lateral view of protoconch showing demarcation of larval and adult shells (bar = 150  $\mu$ m); F. Unattached surface of operculum; G. Attached surface of operculum (bar = 200  $\mu$ m).

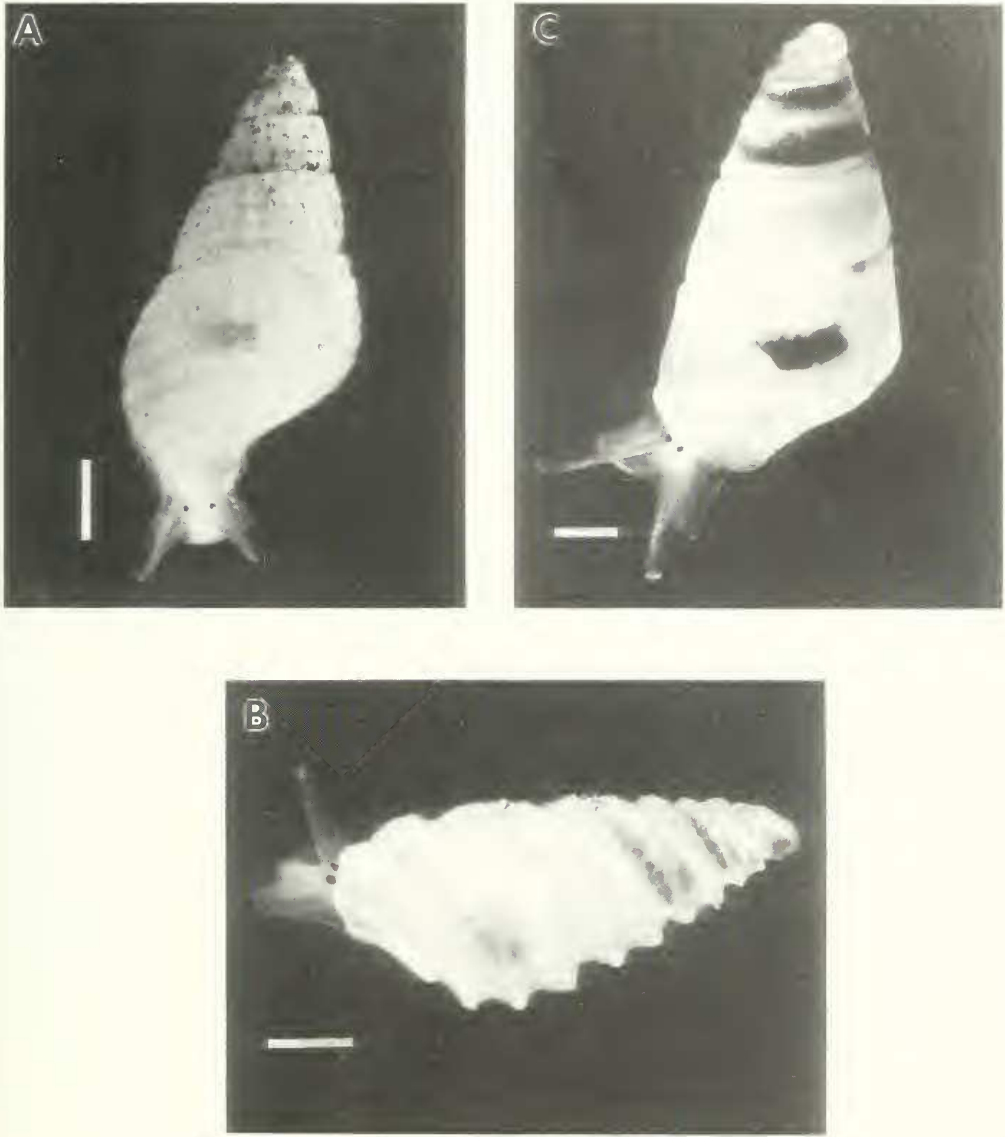


FIG. 10. Living snails of the subfamily Odostominae. A. *Boonea seminuda* (bar = 650  $\mu\text{m}$ ); B. *Odostomia babylonia* (bar = 200  $\mu\text{m}$ ); C. *Odostomia didyma* (bar = 150  $\mu\text{m}$ ).

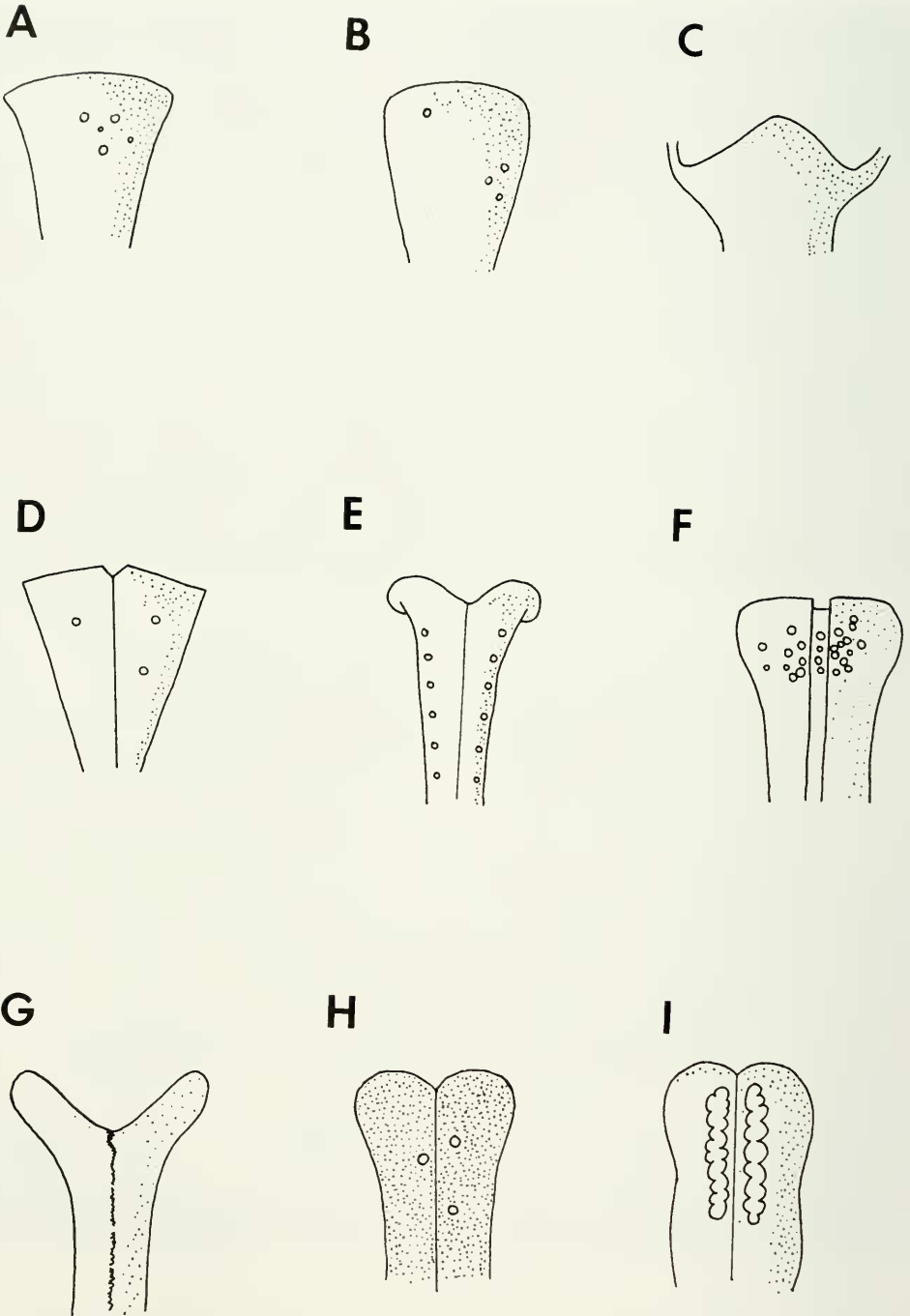


FIG. 11. A. Unnotched mentum of *Boonea seminuda* and *Boonea cincta*; B. Unnotched mentum of *Odostomia babylonica*; C. Unnotched mentum of *Odostomia didyma*; D. Retuse mentum of *Pyramidella mitralis*, *P. sulcata*, and *P. crenulata*; E. Incised mentum of *Turbonilla hemphilli*; F. Retuse mentum of *Houbricka incisa*; G. Incised mentum of *Tathrella iredalei*; H. Emarginate mentum of *Sayella hemphilli*; I. Emarginate mentum of *Petitella crosseana*.

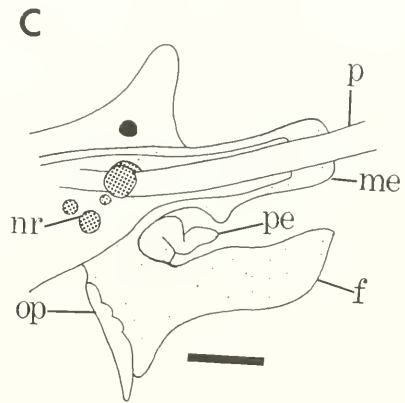
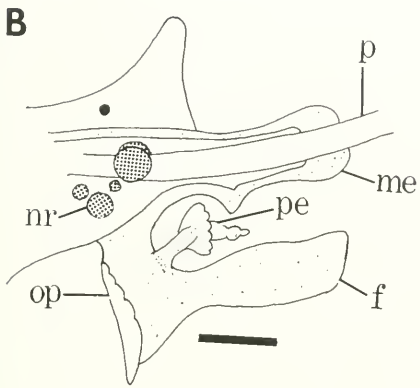
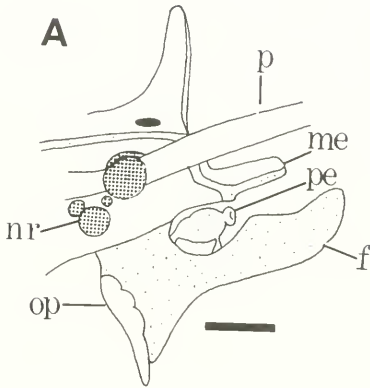


FIG. 12. Diagram of retracted penis configuration and position in: A. *Boonea seminuda* (bar = 250  $\mu$ m); B. *Sayella hemphilli* (bar = 300  $\mu$ m); C. *Petitella crosseana* (bar = 200  $\mu$ m) (f = foot, me = mentum, nr = nerve ring, op = operculum, p = proboscis, pe = penis).

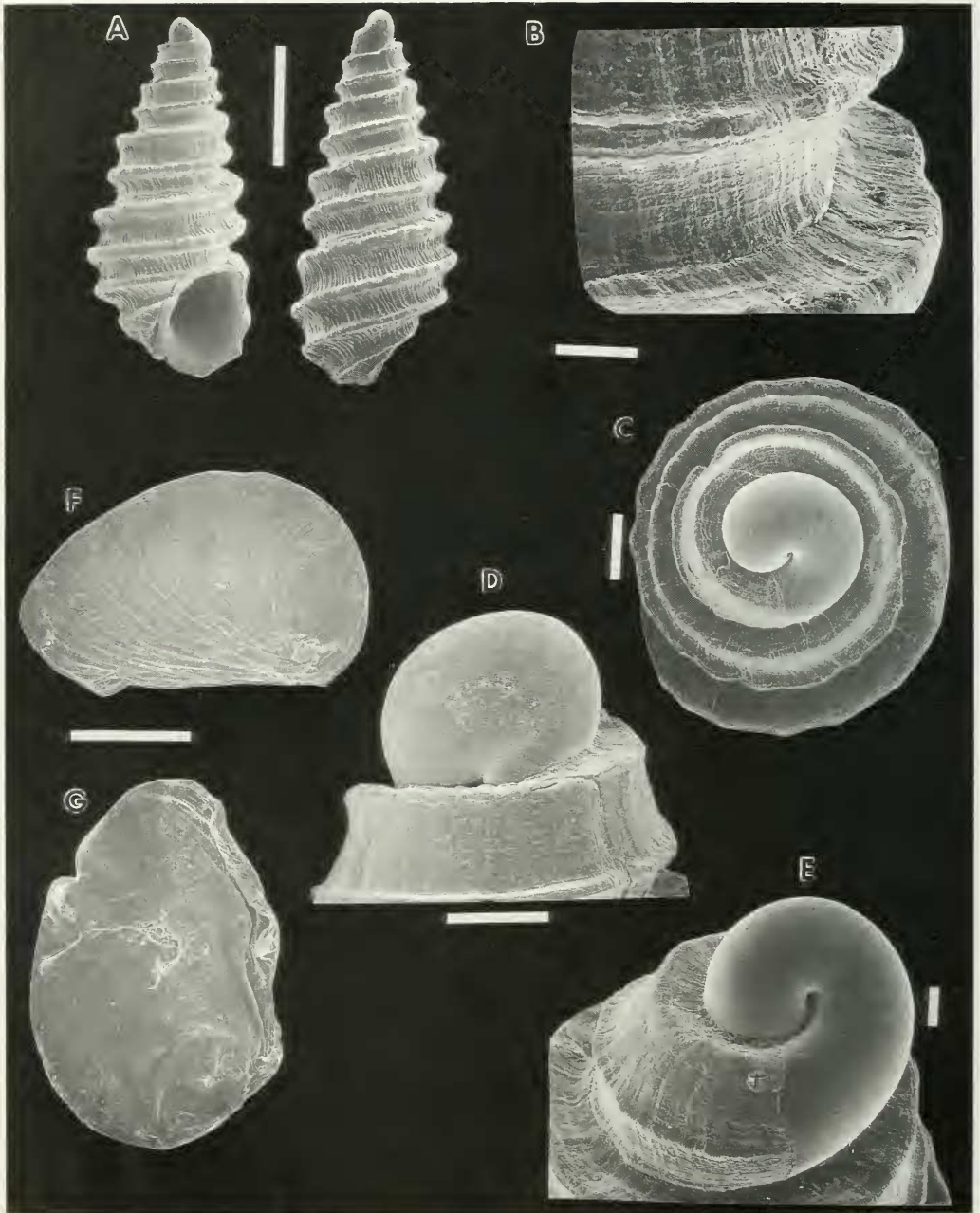


FIG. 13. Shell morphology of *Odostomia babylonica*. SEM microphotographs: A. Apertural and dorsal views of shell (bar = 600  $\mu\text{m}$ ); B. Enlargement of shell's shoulder and suture (bar = 40  $\mu\text{m}$ ); C. Apical view of protoconch (bar = 100  $\mu\text{m}$ ); D. Lateral view of protoconch showing partially exposed earliest portion (bar = 100  $\mu\text{m}$ ); E. Lateral view of protoconch tilted to reveal demarcation of larval and adult shells (bar = 40  $\mu\text{m}$ ); F. Unattached surface of operculum; G. Attached surface of operculum (bar = 150  $\mu\text{m}$ ).



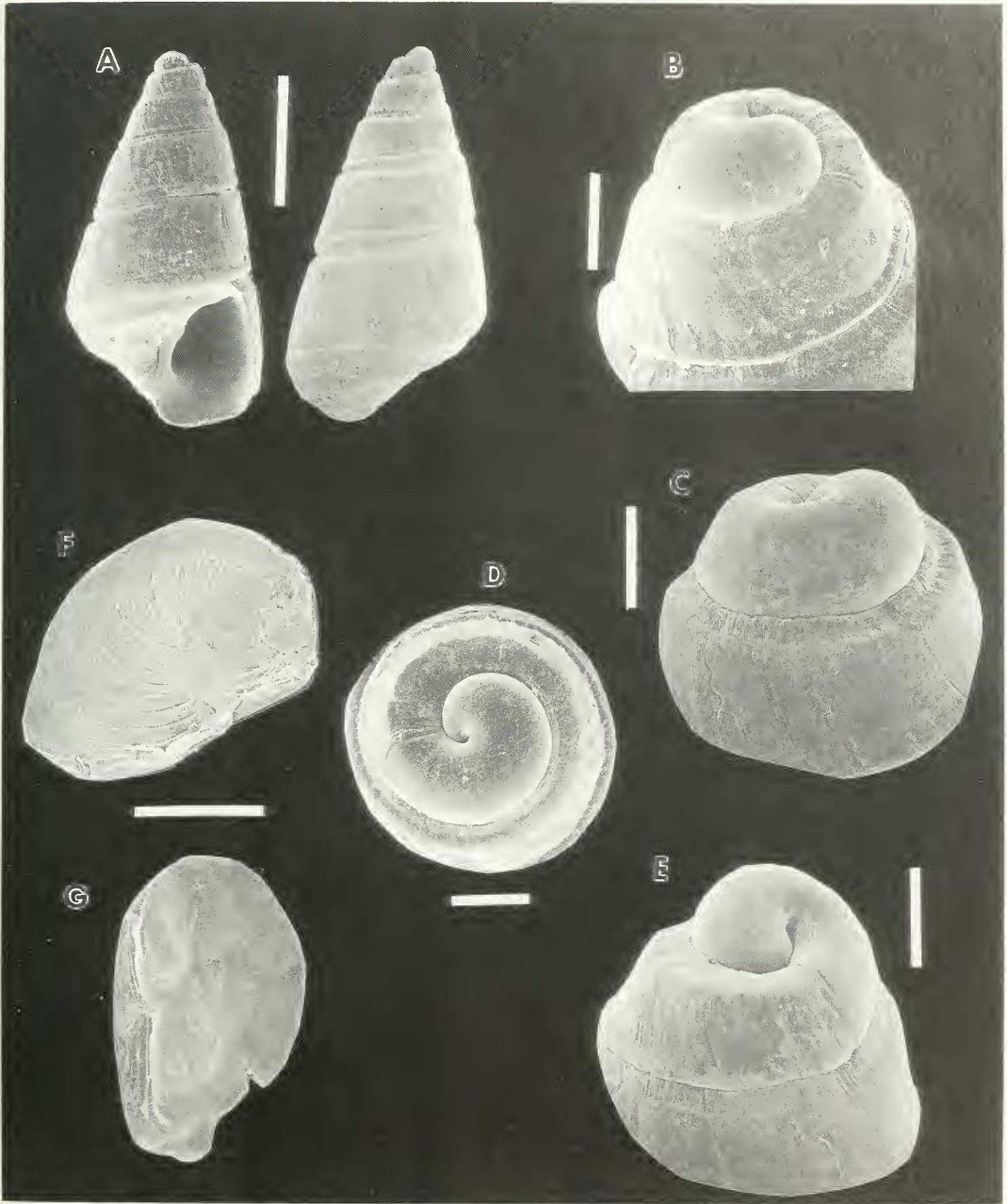


FIG. 14. Shell morphology of *Odostomia didyma*. SEM microphotographs: A. Apertural and dorsal views of shell (bar = 500  $\mu\text{m}$ ); B. Protoconch and oldest adult whorl (bar = 100  $\mu\text{m}$ ); C. Lateral view of protoconch (bar = 100  $\mu\text{m}$ ); D. Apical view of protoconch (bar = 100  $\mu\text{m}$ ); E. Frontal view of protoconch and first adult whorl (note deep shoulder) (bar = 100  $\mu\text{m}$ ); F. Unattached surface of operculum; G. Attached surface of operculum (bar = 150  $\mu\text{m}$ ).

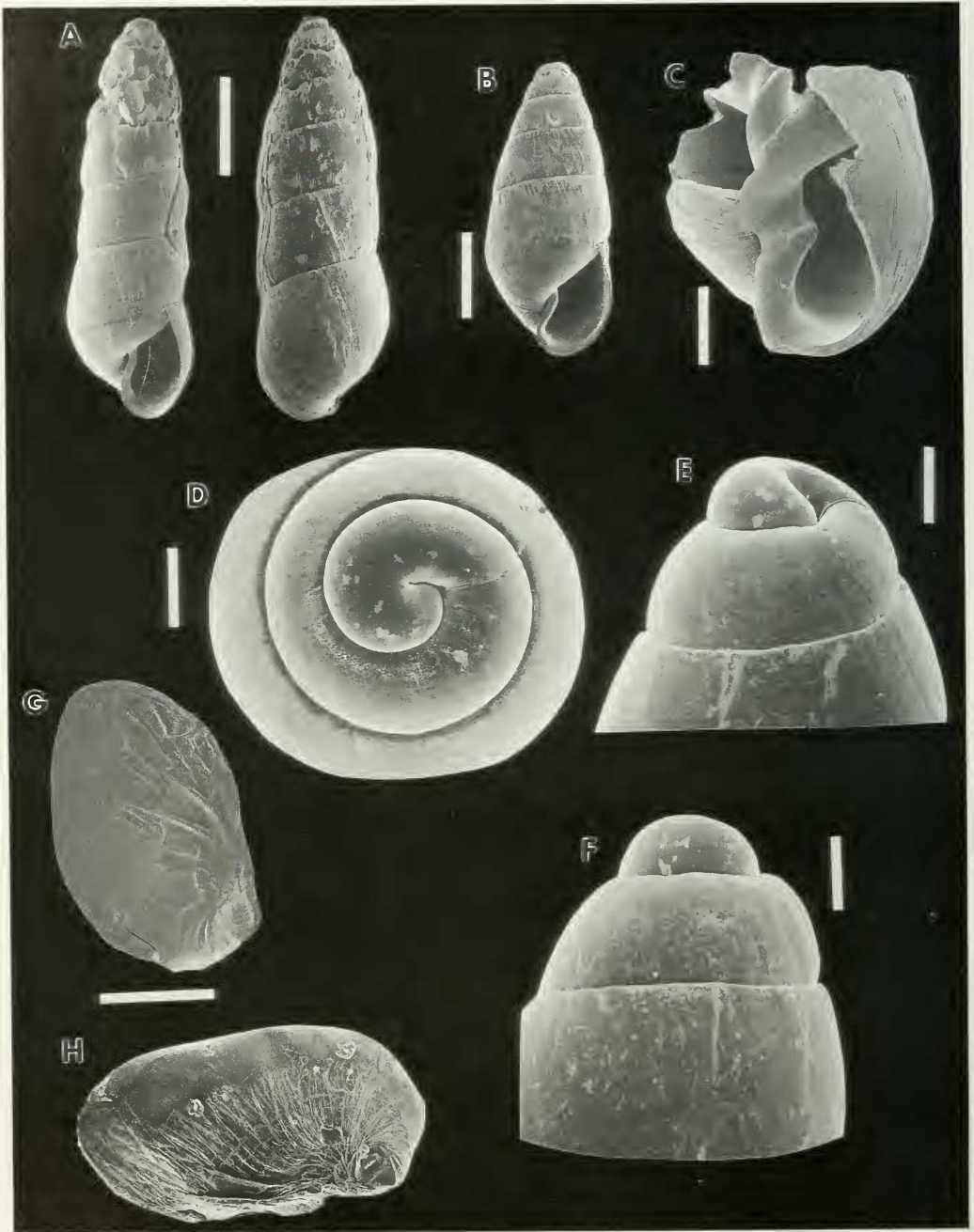


FIG. 15. Shell morphology of *Sayella hemphillii*. SEM microphotographs: A. Apertural and dorsal views (bar = 1 mm); B. Young specimen (note difference between this shell and shell in figure A.) (bar = 1 mm); C. Body whorl cracked open to reveal columellar fold (bar = 400  $\mu$ m); D. Apical view of protoconch (bar = 100  $\mu$ m); E. Frontal view of protoconch (bar = 100  $\mu$ m); F. Lateral view of protoconch (bar = 100  $\mu$ m); G. Attached surface of operculum; H. Unattached surface of operculum (bar = 400  $\mu$ m).

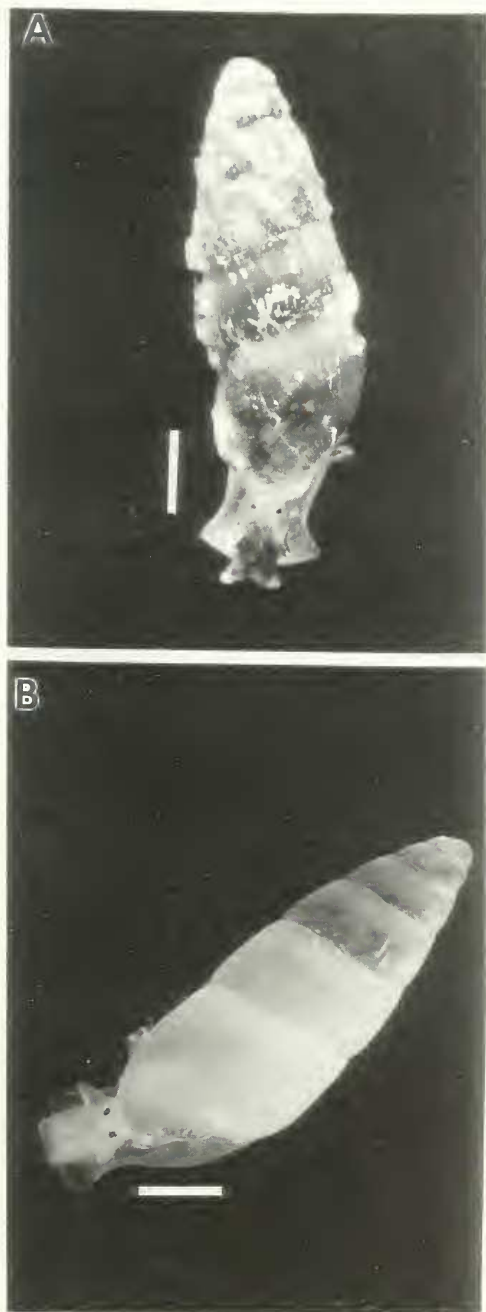


FIG. 16. A. *Sayella hemphillii* (bar = 1 mm); B. *Petitella crosseana* (bar = 500  $\mu$ m).

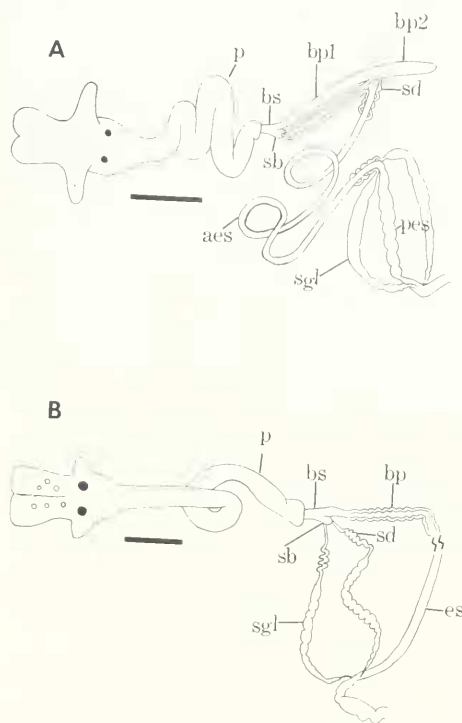


FIG. 17. A. Diagram of the alimentary tract of *Sayella hemphillii* (bar = 1 mm); B. Diagram of alimentary tract of *Petitella crosseana* (bar = 500  $\mu$ m) (aes = anterior esophagus, bp = buccal pump, bp1 = buccal pump 1, bp2 = buccal pump 2, bs = buccal sac, es = esophagus, p = proboscis, pes = posterior esophagus, sb = stylet bulb, sd = salivary gland duct, sgl = salivary gland).

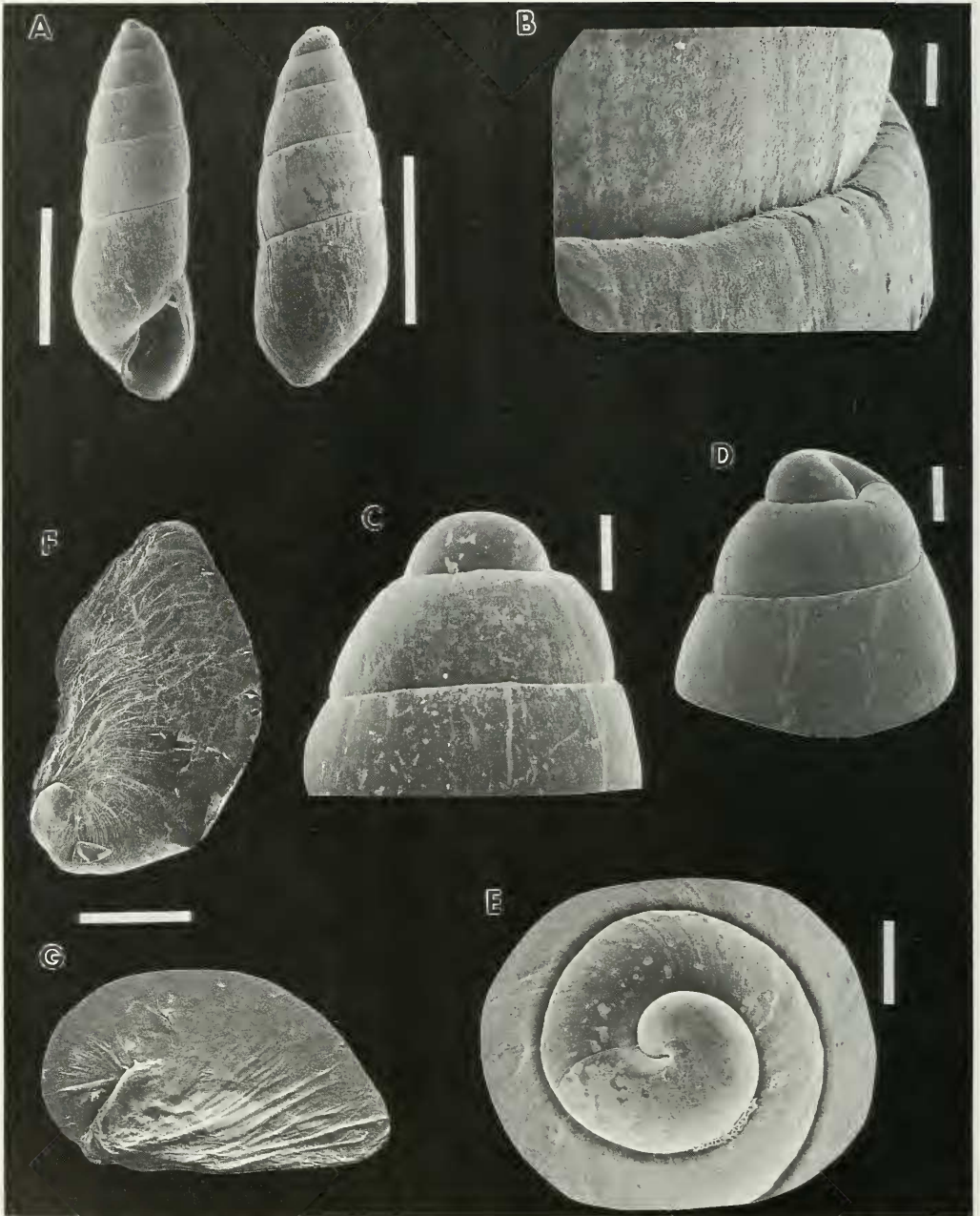


FIG. 18. Shell morphology of *Petittella crosseana*. SEM microphotographs: A. Apertural and dorsal views (bar = 1 mm); B. Enlargement of the shell's shoulder and suture (bar = 20  $\mu\text{m}$ ); C. Lateral view of protoconch and earliest adult whorls (bar = 100  $\mu\text{m}$ ); D. Frontal view of protoconch (bar = 100  $\mu\text{m}$ ); E. Apical view of protoconch (bar = 100  $\mu\text{m}$ ); F. Unattached surface of operculum; G. Attached surface of operculum (bar = 200  $\mu\text{m}$ ).

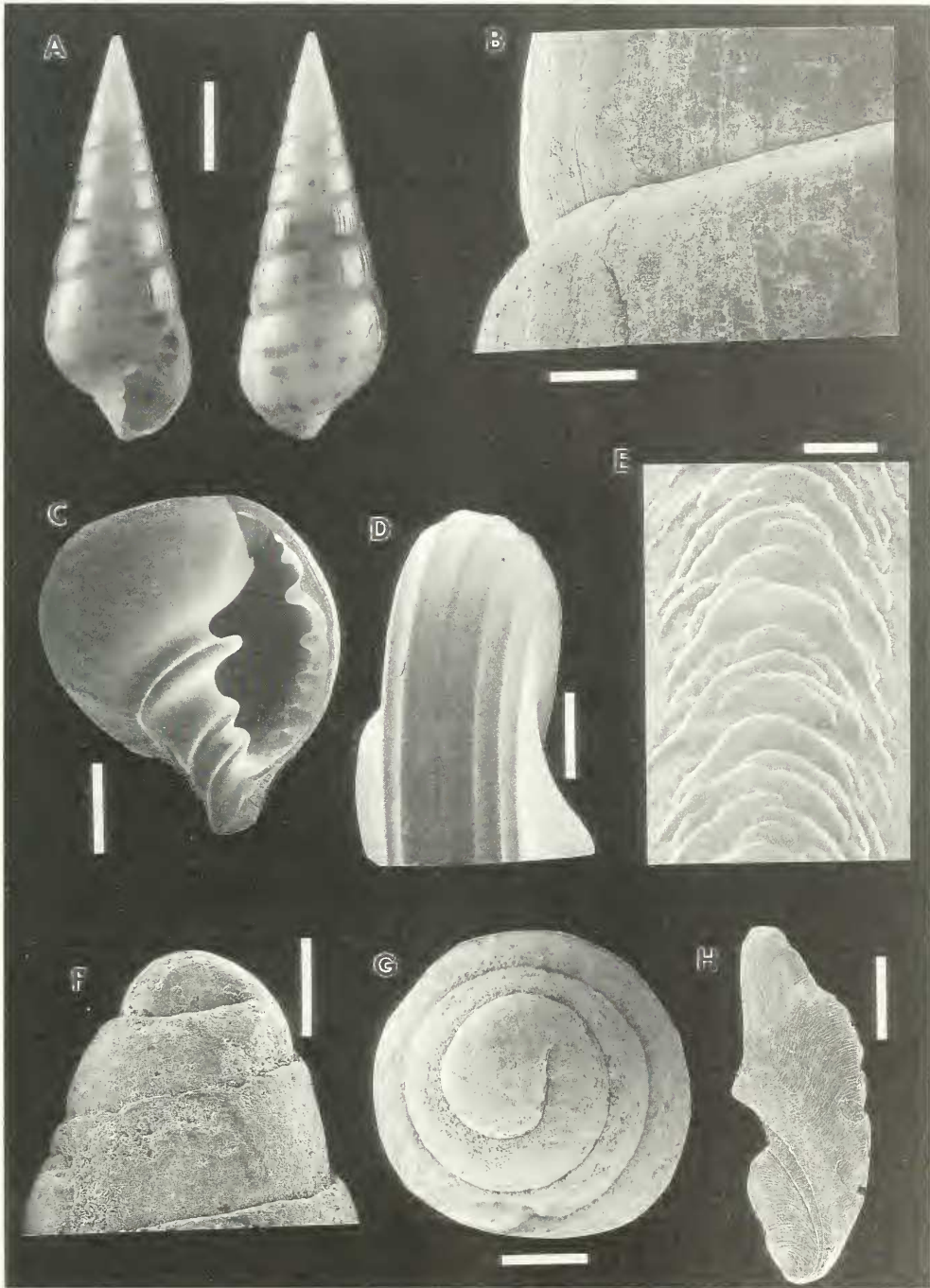


FIG. 19. Shell morphology of *Pyramidella sulcata*. A. Apertural and dorsal view of shell (bar = 4 mm); SEM microphotographs: B. Suture and surface microstructure (note growth lines) (bar = 600  $\mu$ m); C. Shell aperture with columellar folds and mature, well-developed palatal teeth (bar = 2 mm); D. Ridges of largest columellar fold (bar = 200  $\mu$ m); E. Columellar fold ridges, composed of imbricated plates (bar = 10  $\mu$ m); F. Lateral view of partially eroded protoconch (bar = 200  $\mu$ m); G. Apical view of protoconch (bar = 200  $\mu$ m); H. Unattached surface of operculum (bar = 1 mm).

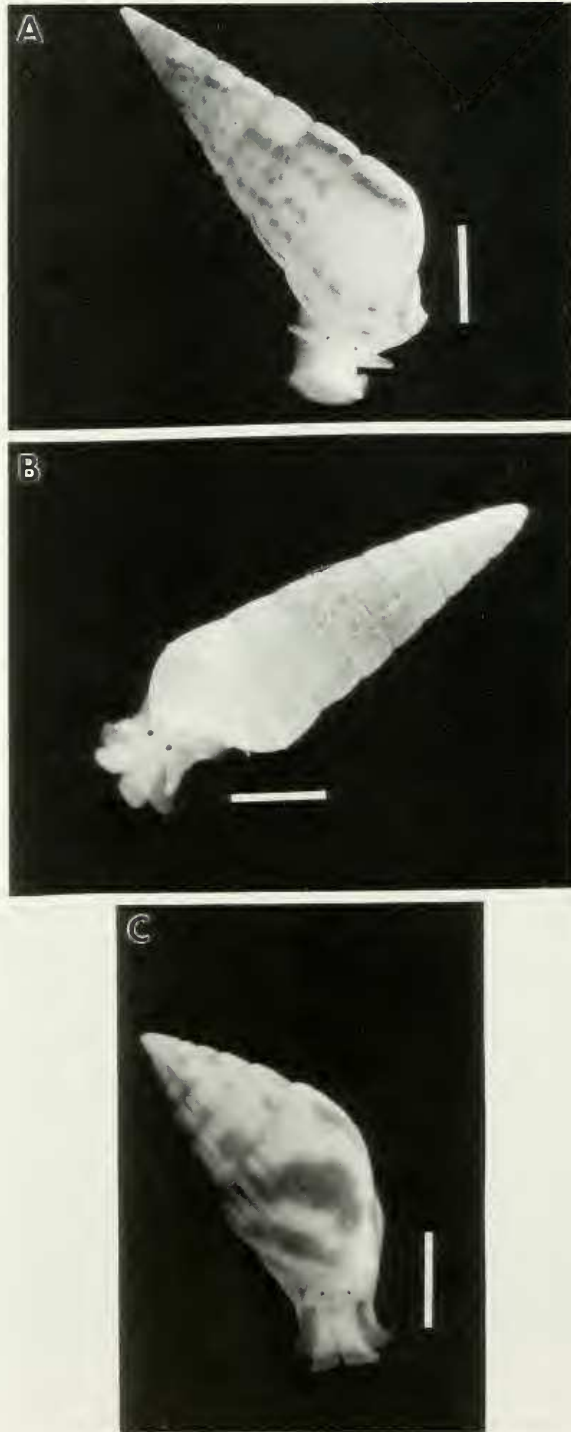


FIG. 20. Living snails of the subfamily Pyramidellinae. A. *Pyramidella sulcata* (bar = 3 mm); B. *Pyramidella crenulata* (bar = 2 mm) C. *Pyramidella mitralis* (bar = 3 mm).

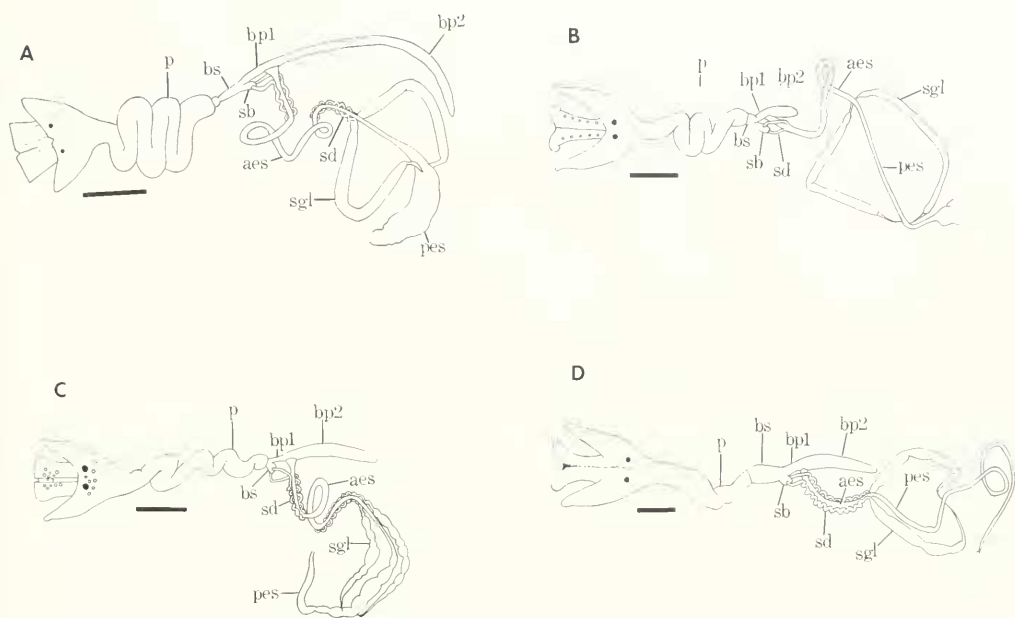


FIG. 21. Diagram pyramidellid alimentary tracts. A. *Pyramidella mitralis*, *P. sulcata*, *P. crenulata* (bar = 1 mm); B. *Turbonilla hemphilli* (bar = 500  $\mu$ m); C. *Houbricka incisa* (bar = 500  $\mu$ m); D. *Tathrella iredalei* (bar = 300  $\mu$ m) (aes = anterior esophagus, bp1 = buccal pump 1, bp2 = buccal pump 2, bs = buccal sac, p = proboscis, pes = posterior esophagus, sb = stylet bulb, sd = salivary gland duct, sgl = salivary gland).

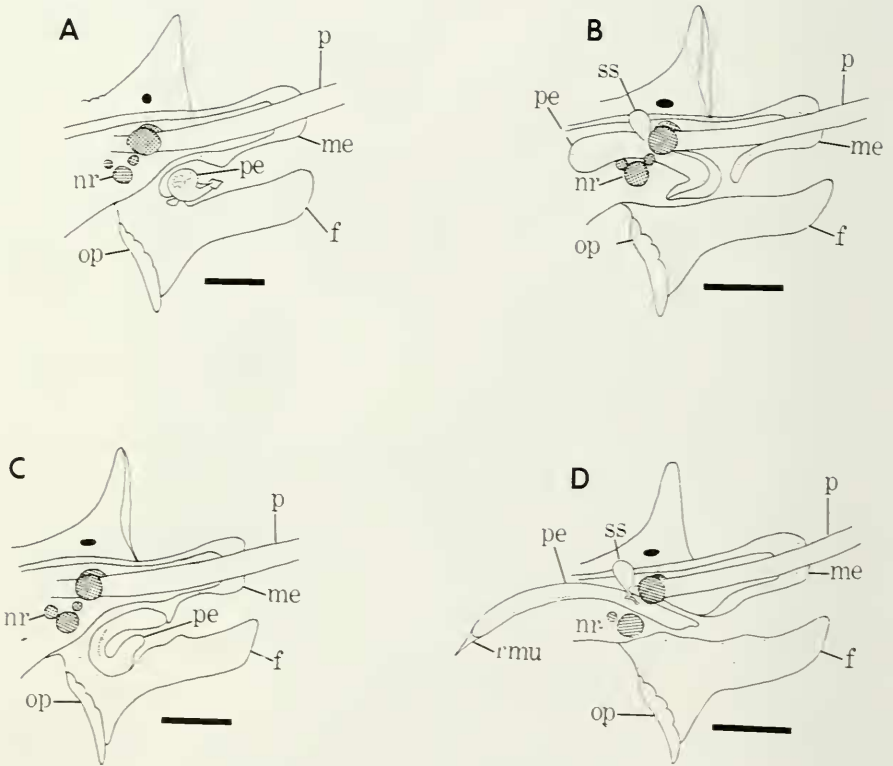


FIG. 22. Diagram of pyramidellid retracted penes *in situ*. A. *Pyramidella sulcata*, *P. crenulata*, and *P. mitralis* (bar = 1 mm); B. *Turbonilla hemphilli* (bar = 500  $\mu$ m); C. *Houbrieka incisa* (bar = 400  $\mu$ m); D. *Tathrella iredalei* (bar = 300  $\mu$ m) (f = foot, me = mentum, nr = nerve ring, op = operculum, p = proboscis, pe = penis, rmu = retractor muscle, ss = sperm sac).



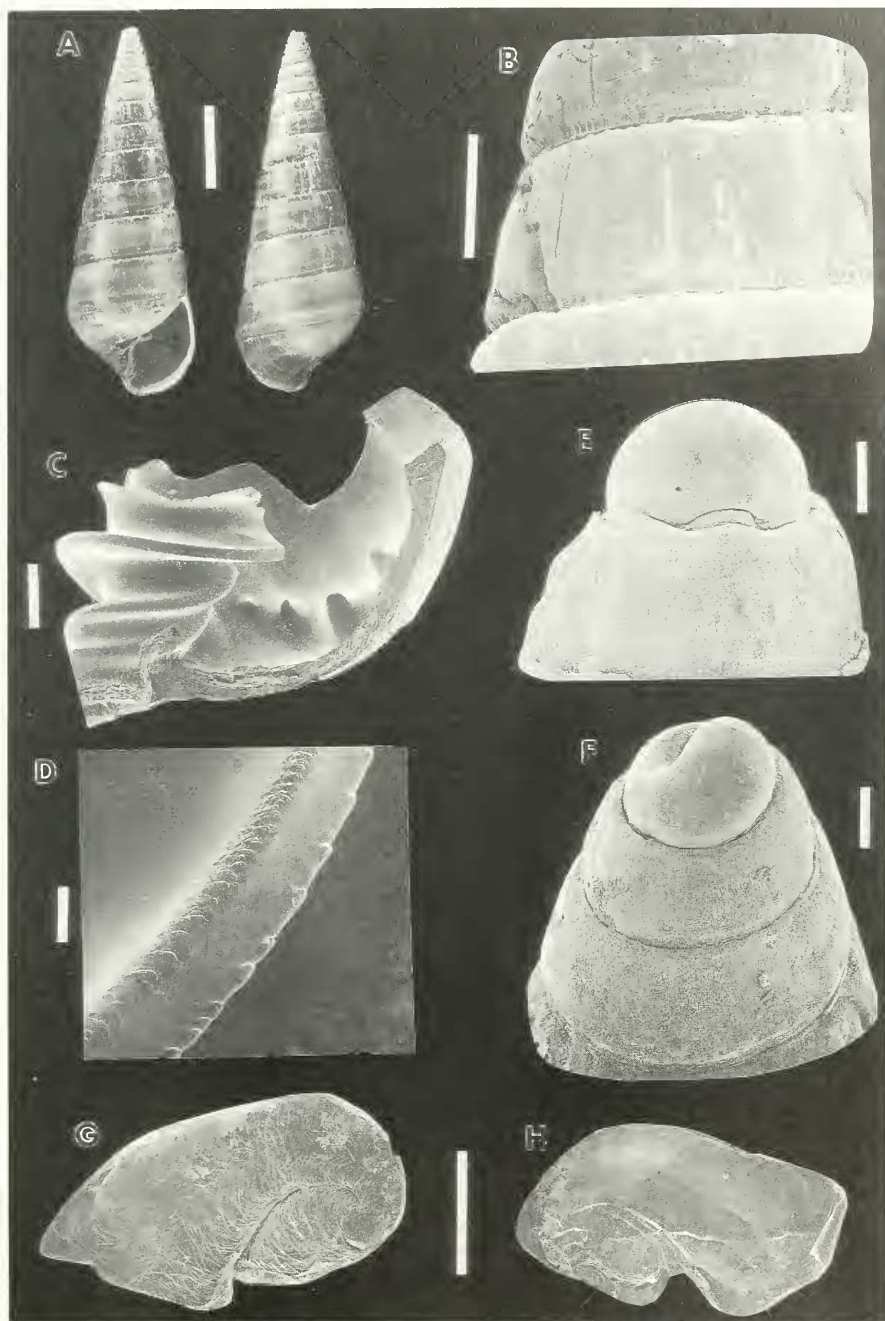


FIG. 23. Shell morphology of *Pyramidella crenulata*. A. Apertural and dorsal views of shell (bar = 3 mm); SEM microphotographs: B. Sutures and exterior surface of shell (bar = 500  $\mu$ m); C. Portion of broken body whorl revealing mature palatal teeth and columellar folds (bar = 400  $\mu$ m); D. Single ridge of non-overlapping and overlapping plates on largest columellar fold (bar = 40  $\mu$ m); E. Lateral view of protoconch (bar = 100  $\mu$ m); F. Dorsal view of protoconch (bar = 125  $\mu$ m); G. Unattached surface of operculum; H. Attached surface of operculum (bar = 430  $\mu$ m).

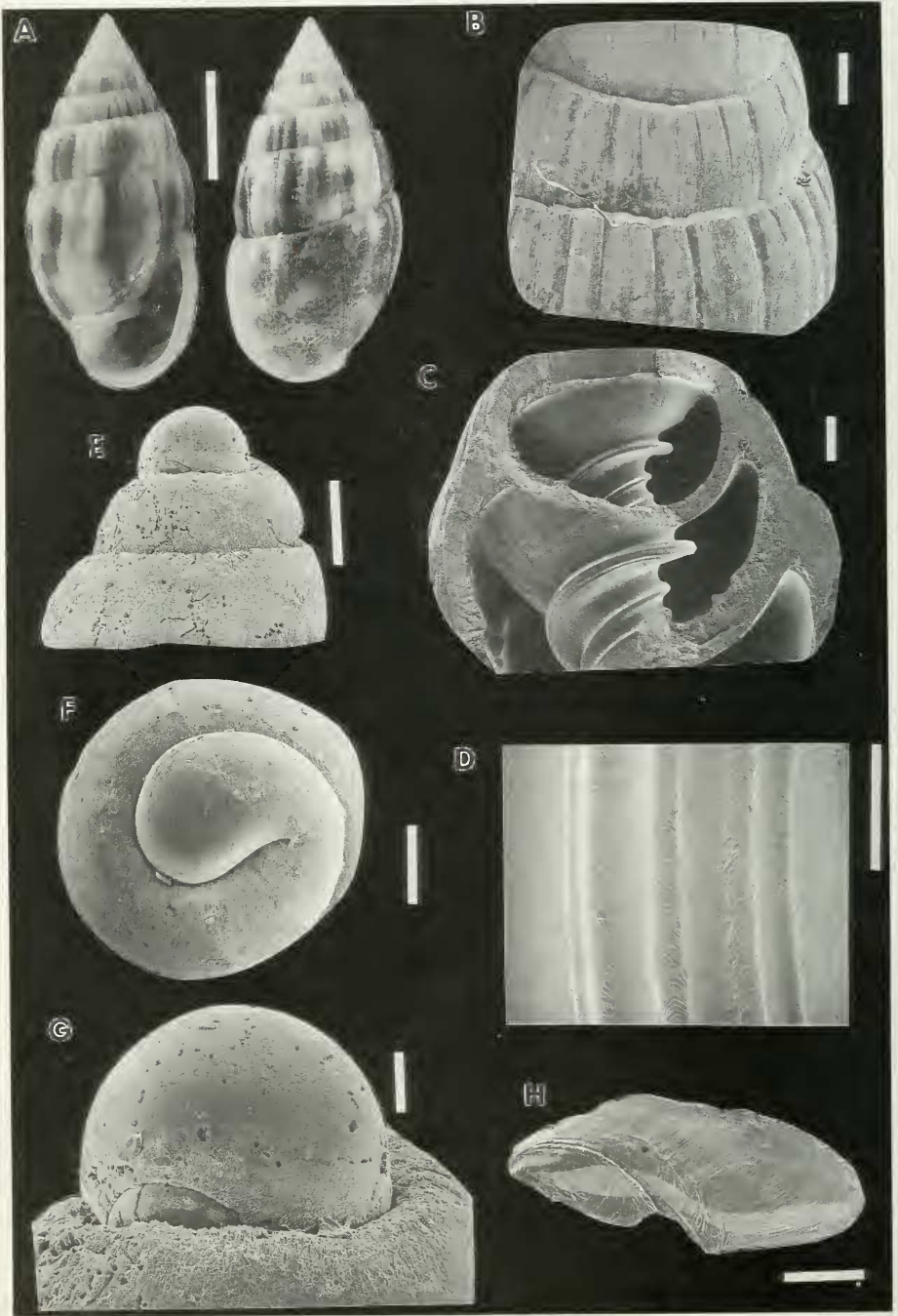


FIG. 24. Shell morphology of *Pyramidella mitralis*. A. Apertural and dorsal views of shell (bar = 4 mm); SEM microphotographs: B. Sutures and surface sculpture of shell (bar = 200  $\mu$ m); C. Shell cut away to expose columellar folds (bar = 400  $\mu$ m); D. Ridges of largest columellar fold (bar = 100  $\mu$ m); E. Lateral view of protoconch (bar = 200  $\mu$ m); F. Apical view of protoconch (bar = 125  $\mu$ m); G. Enlargement of tilted, lateral view of protoconch with a portion of earliest whorl visible (bar = 40  $\mu$ m); H. Attached surface of operculum (bar = 1 mm).

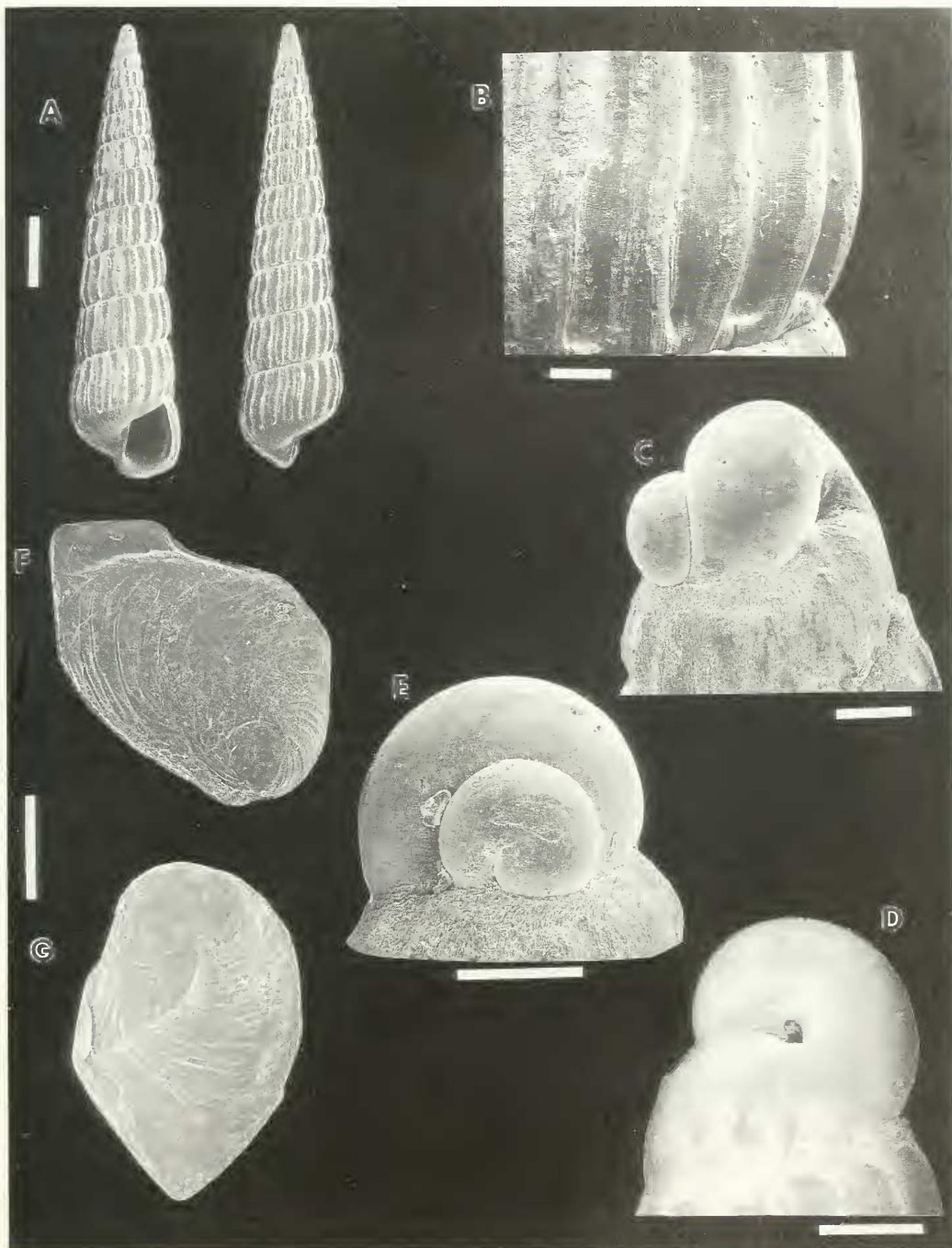


FIG. 25. Shell morphology of *Turbonilla hemphilli*. A. Apertural and dorsal views of shell (bar = 1.5 mm); SEM microphotographs: B. Enlargement of whorl immediately dorsal to body whorl (note ribbing) (bar = 125  $\mu$ m); C. Frontal view of protoconch (bar = 100  $\mu$ m); D. Lateral view of protoconch (bar = 100  $\mu$ m); E. Lateral view of protoconch showing portion of earliest whorl (bar = 100  $\mu$ m); F. Unattached surface of operculum; G. Attached surface of operculum (bar = 250  $\mu$ m).

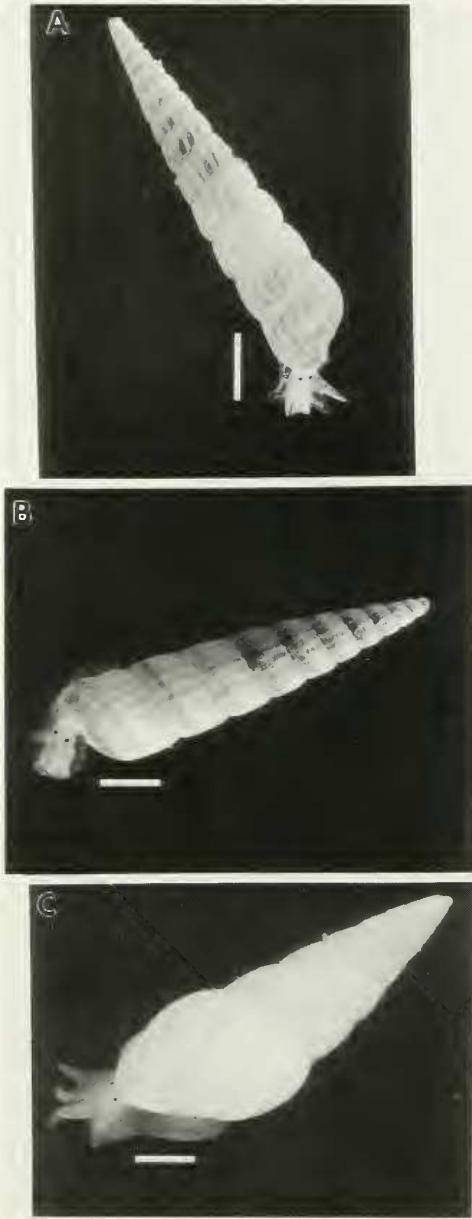


FIG. 26. Living snails of the subfamily Turbonillinae. A. *Turbonilla hemphilli* (bar = 1.5 mm); B. *Houbricka incisa* (bar = 1 mm); C. *Tathrella iredalei* (bar = 800  $\mu$ m).

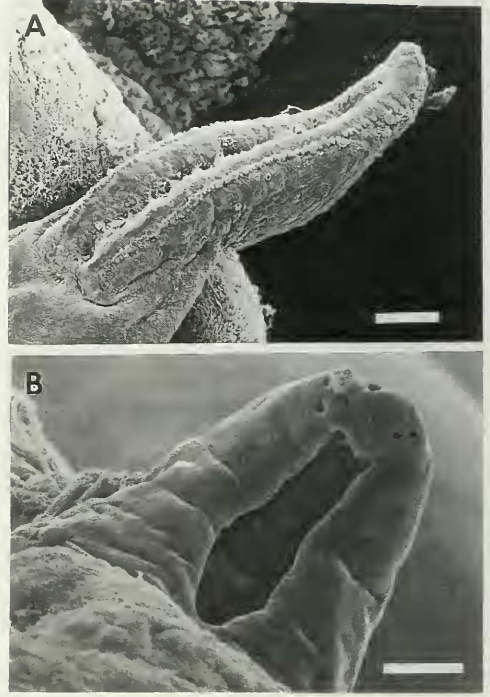


FIG. 27. A. SEM microphotograph of anterior portion of penis of *Turbonilla hemphilli* (note medial groove and lateral cuticular hooks) (bar = 75  $\mu$ m); B. SEM microphotograph of anterior tip of penis of *Houbricka incisa* (bar = 10  $\mu$ m).

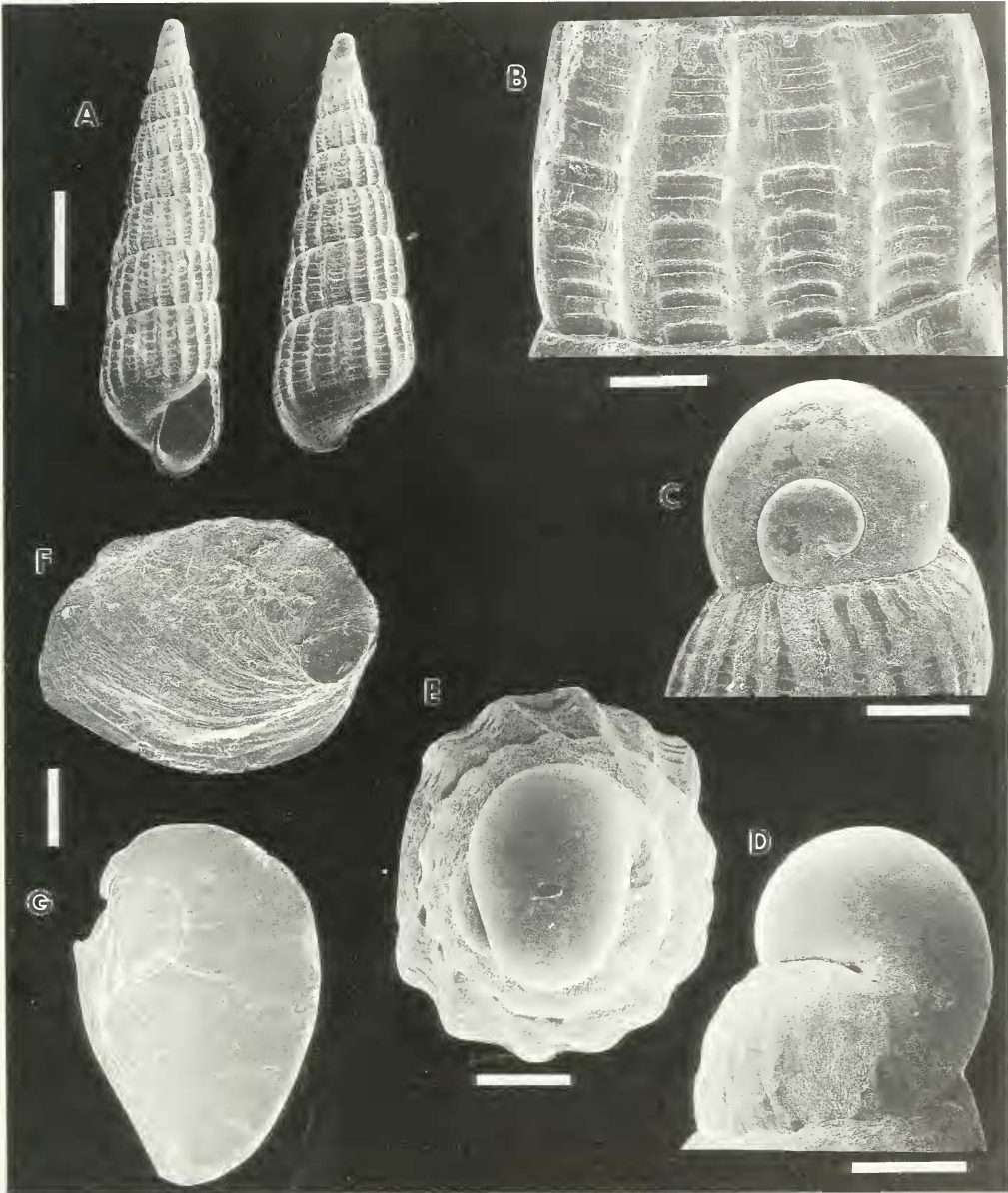


FIG. 28. Shell morphology of *Houbricka incisa*. SEM microphotographs: A. Apertural and dorsal views (bar = 1.25 mm); B. Enlargement of the whorl immediately dorsal to body whorl (note costae and intercostal grooves) (bar = 150  $\mu$ m); C. Lateral view of earliest larval whorls (bar = 100  $\mu$ m); D. Lateral view of protoconch and earliest adult whorl (bar = 100  $\mu$ m); E. Apical view of protoconch (bar = 100  $\mu$ m); F. Unattached surface of operculum; G. Attached surface of operculum (bar = 175  $\mu$ m).

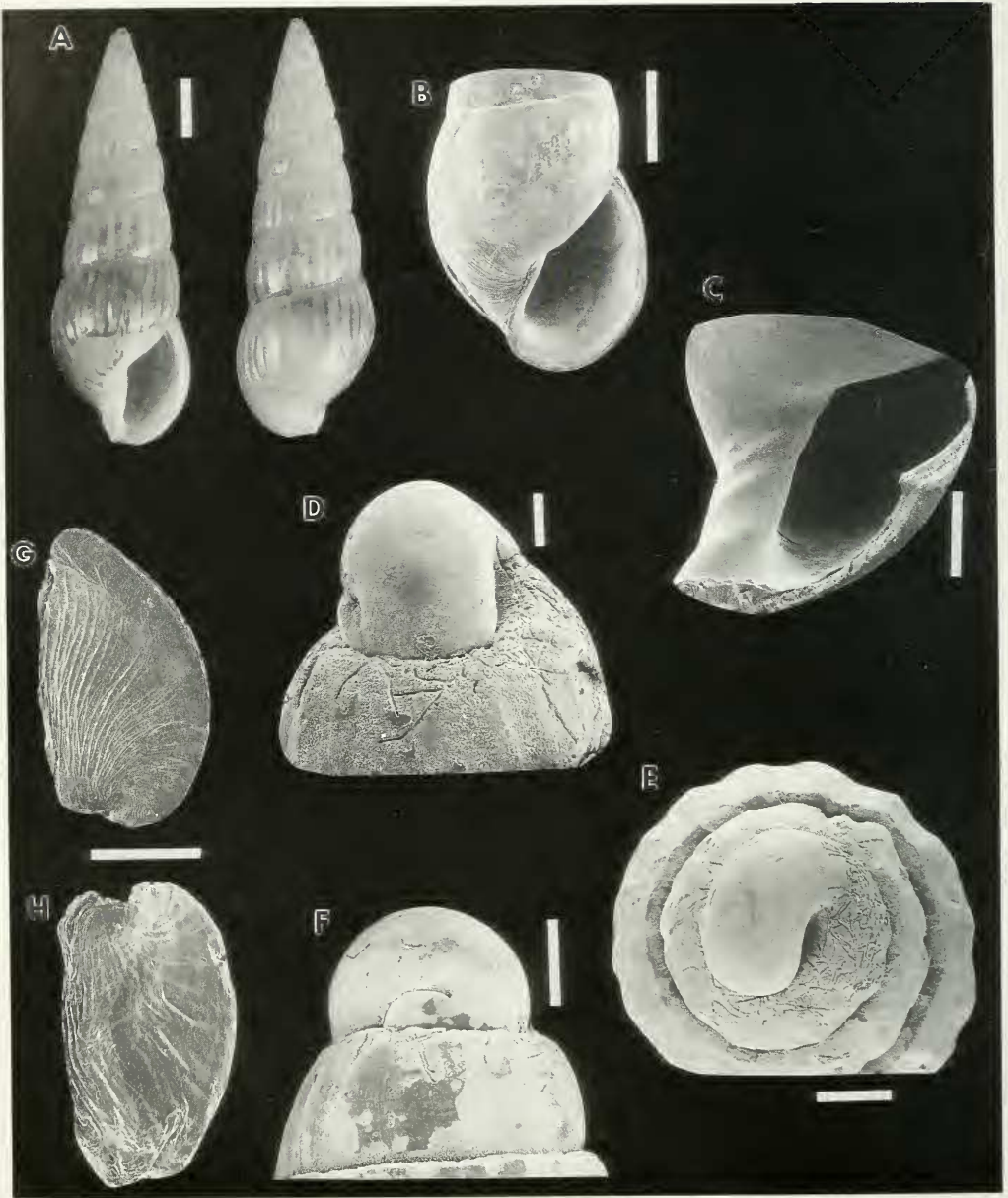


FIG. 29. Shell morphology of *Tathrella iredalei*. A. Apertural and dorsal views (bar = 1 mm); SEM microphotographs: B. Body whorl (bar = 1 mm); C. Shell broken to reveal swellings on columella located within the whorl immediately dorsal to body whorl (bar = 400  $\mu$ m); D. Frontal view of protoconch (bar = 50  $\mu$ m); E. Apical view of protoconch (bar = 100  $\mu$ m); F. Lateral view of protoconch with early whorl partially exposed (bar = 100  $\mu$ m); G. Unattached surface of operculum; H. Attached surface of operculum (bar = 400  $\mu$ m).

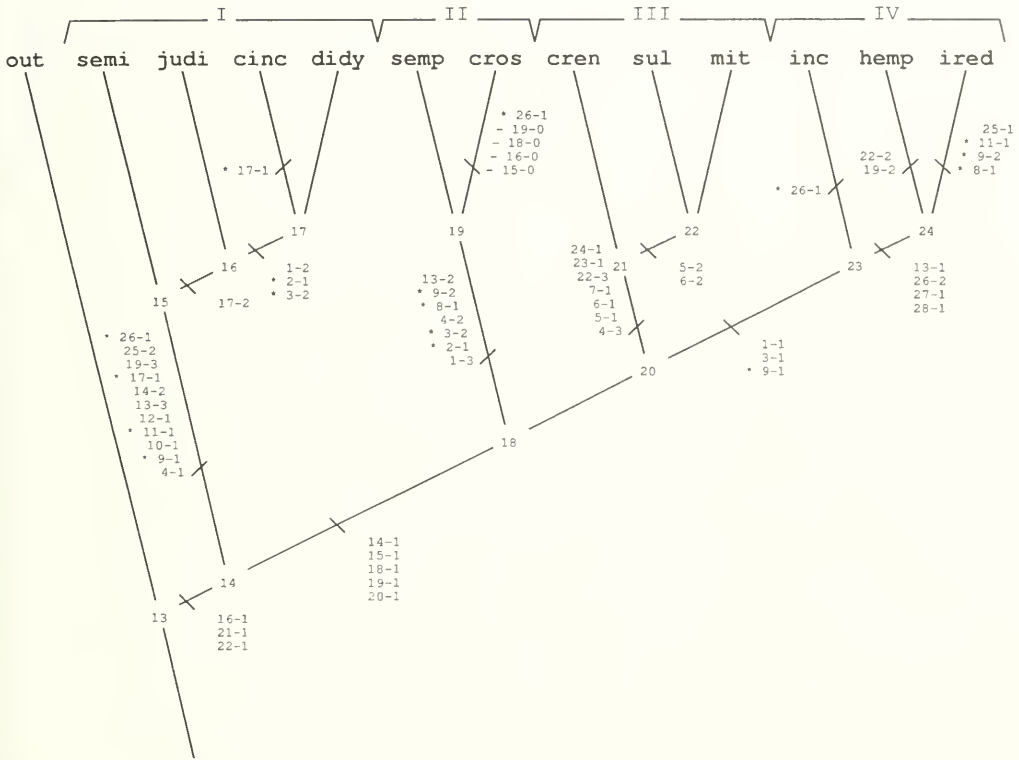


FIG. 30. One of six cladograms resulting from analysis of character matrix in Table 3 (OUT = Amathinidae, CINC = *Chrysallida cincta*, SEMI = *Boonea seminuda*, JUDI = *Odostomia babylonica*, DIDY = *Odostomia didyma*, SEMP = *Sayella hemphillii*, CROS = *Petitella crosseana*, SUL = *Pyramidella sulcata*, CREN = *P. crenulata*, MIT = *Pyramidella mitralis*, HEMP = *Turbonilla hemphilli*, INC = *Houbricka incisa*, IRED = *Tathrella iredalei*).

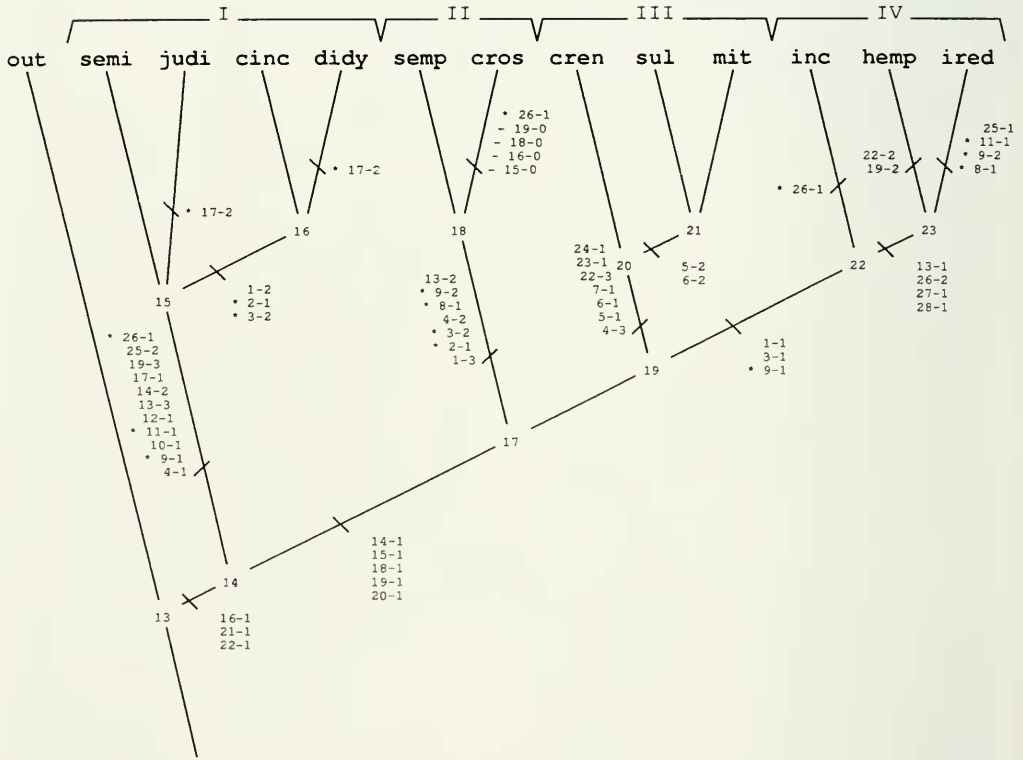


FIG. 31. One of six cladograms resulting from analysis of character matrix in Table 3 (OUT = Amathinidae, CINC = *Chrysalida cincta*, SEMI = *Boonea seminuda*, JUDI = *Odostomia babylonica*, DIDY = *Odostomia didyma*, SEMP = *Sayella hemphillii*, CROS = *Petitella crosseana*, SUL = *Pyramidella sulcata*, CREN = *P. crenulata*, MIT = *Pyramidella mitralis*, HEMP = *Turbonilla hemphilli*, INC = *Houbricka incisa*, IRED = *Tathrella iredalei*).



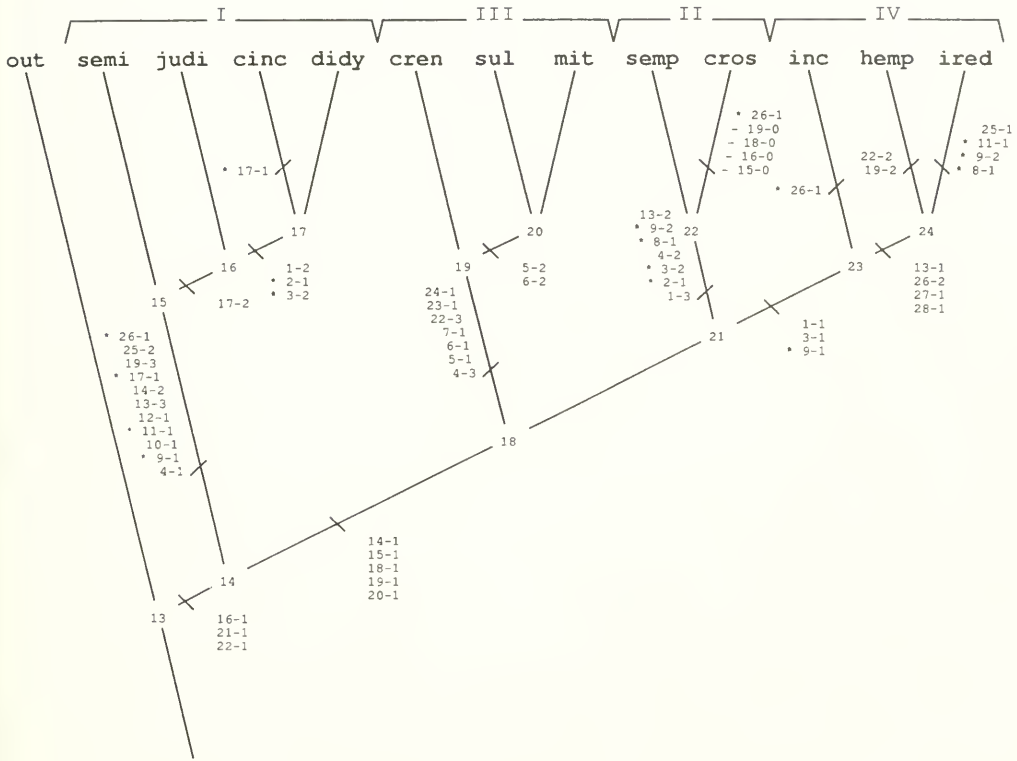


FIG. 32. One of six cladograms resulting from analysis of character matrix in Table 3 (OUT = Amathinidae, CINC = *Chrysalida cincta*, SEMI = *Boonea seminuda*, JUDI = *Odostomia babylonica*, DIDY = *Odostomia didyma*, SEMP = *Sayella hemphillii*, CROS = *Petitella crosseana*, SUL = *Pyramidella sulcata*, CREN = *P. crenulata*, MIT = *Pyramidella mitralis*, HEMP = *Turbonilla hemphilli*, INC = *Houbricka incisa*, IRED = *Tathrella iredalei*).

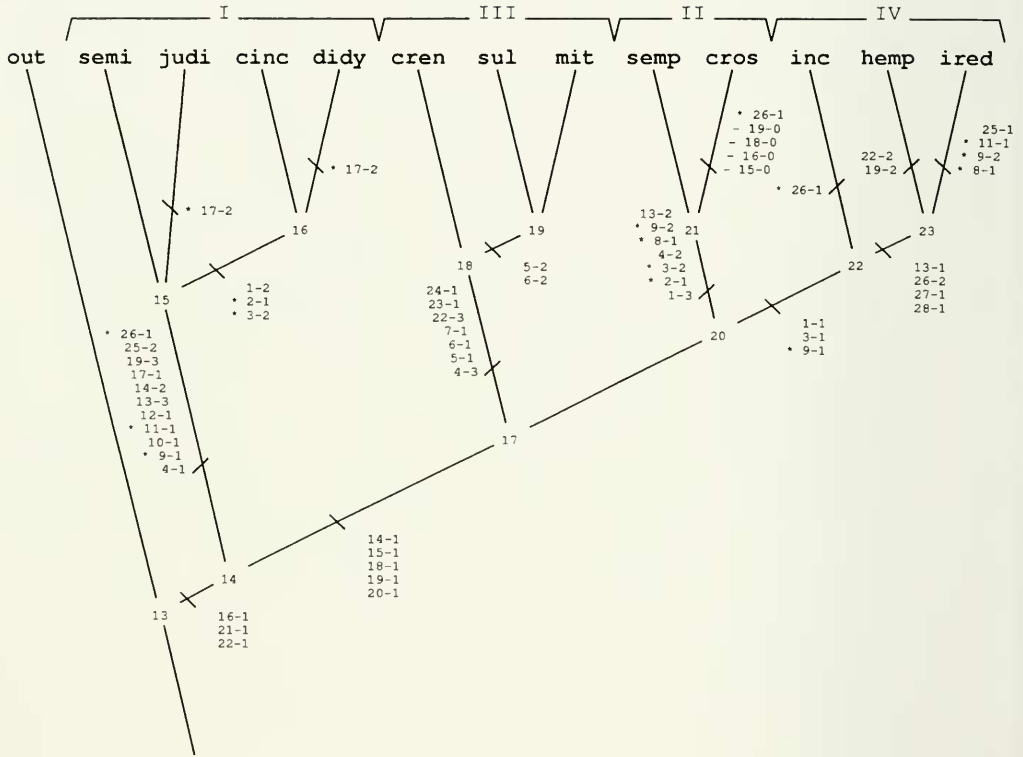


FIG. 33. One of six cladograms resulting from analysis of character matrix in Table 3 (OUT = Amathinidae, CINC = *Chrysallida cincta*, SEMI = *Boonea seminuda*, JUDI = *Odostomia babylonica*, DIDY = *Odostomia didyma*, SEMP = *Sayella hemphillii*, CROS = *Petitella crosseana*, SUL = *Pyramidella sulcata*, CREN = *P. crenulata*, MIT = *Pyramidella mitralis*, HEMP = *turbonilla hemphilli*, INC = *Houbricka incisa*, IRED = *Tathrella iredalei*).

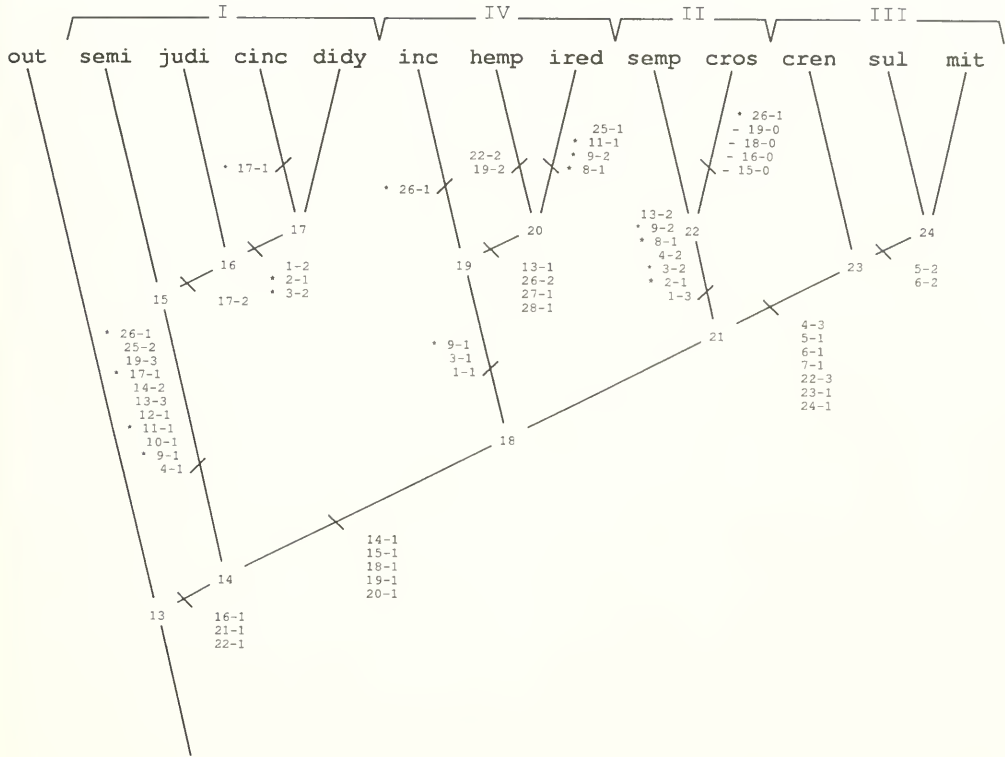


FIG. 34. One of six cladograms resulting from analysis of character matrix in Table 3 (OUT = Amathinidae, CINC = *Chrysalida cincta*, SEMI = *Boonea seminuda*, JUDI = *Odostomia babylonica*, DIDY = *Odostomia didyma*, SEMP = *Sayella hemphillii*, CROS = *Petitella crosseana*, SUL = *Pyramidella sulcata*, CREN = *P. crenulata*, MIT = *Pyramidella mitralis*, HEMP = *Turbonilla hemphillii*, INC = *Houbrieka incisa*, IRED = *Tathrella iredalei*).

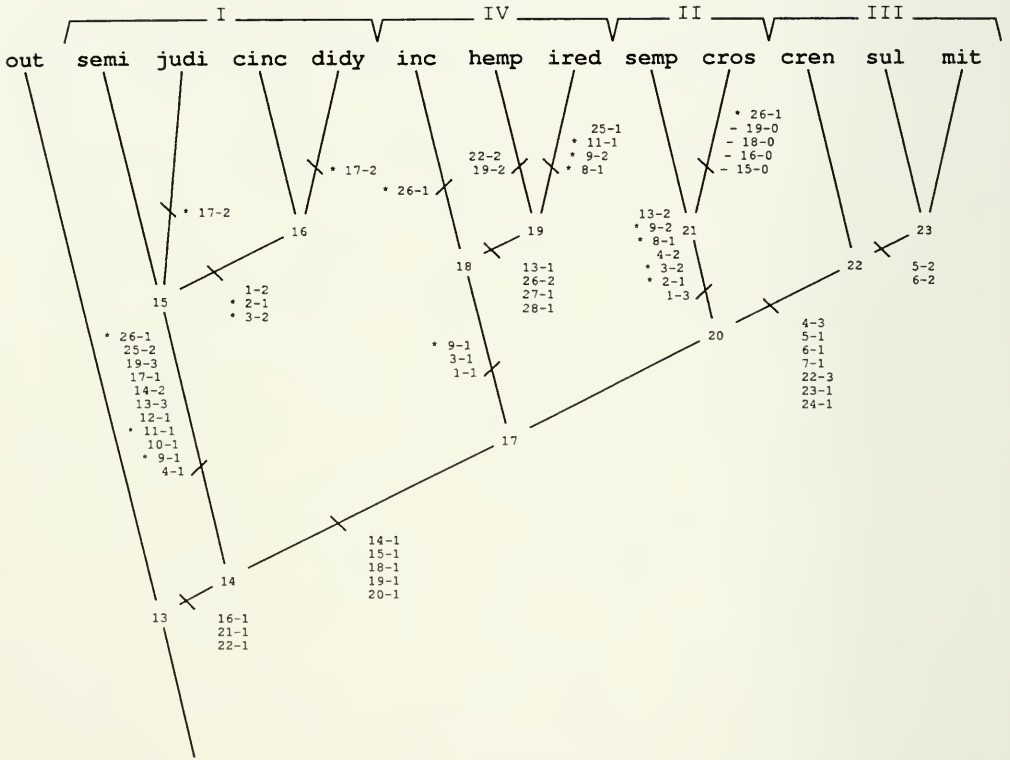


FIG. 35. One of six cladograms resulting from analysis of character matrix in Table 3 (OUT = Amathinidae, CINC = *Chrysallida cincta*, SEMI = *Boonea seminuda*, JUDI = *Odostomia babylonica*, DIDY = *Odostomia didyma*, SEMP = *Sayella hemphillii*, CROS = *Petitella crosseana*, SUL = *Pyramidella sulcata*, CREN = *P. crenulata*, MIT = *Pyramidella mitralis*, HEMP = *Turbonilla hemphilli*, INC = *Houbricka incisa*, IRED = *Tathrella iredalei*).



## TAXA DIAGNOSES AND DESCRIPTIONS

Family Pyramidellidae Gray, 1840  
 Subfamily Odostominae Pelseener, 1928  
 Genus *Boonea* Robertson, 1978

*Boonea* Robertson, 1978:364. Type-species:  
*Jaminia seminuda* C. B. Adams, 1839,  
 by original designation.

*Diagnosis:* Shell thick, chalky white, conical, 3–5 mm in length, with 4–5 adult whorls. Whorls with or without spiral cords, axial ribs or both. Body whorl 50% of shell length. Umbilicus minute or absent. Protoconch smooth, sinistrally heterostrophic oriented 120°–130° to teleoconch, partially submerged in first adult whorl. Aperture auriform, with single acute columellar fold. Operculum tan or brown, auriform, paucispiral, with subcentric nucleus. Head-foot white and often lentiginous. Foot narrowing posterior to propodium, widening and narrowing again posteriorly to a blunt tip. Posterior pedal gland producing attachment thread. Tentacles subtriangular, connate, ventro-laterally folded; tentacular pads present. Eyes subepithelial, on median side of tentacles. Mentum unnotched, not bifurcate. Introvert-proboscis aperture on ventral side of head, dorsal to mentum base. Introvert joining buccal sac, which is composed of sucker, mouth, sheathed stylet with separate opening, oral tube, and stylet bulb. Buccal sac joining buccal pump, which is divided into anterior (bp1) and posterior sections (bp2). Esophagus originating on ventral surface of bp1-bp2 juncture. Salivary gland ducts entering gut and extending parallel to one another within walls of bp1 and entering stylet bulb without exiting alimentary tract. Globose penis tapering posteriorly and located outside and ventral to nerve ring. Uncuticularized spermatophores attached to species-specific location (e.g., snail's neck or outside last whorl) prior to transfer to mate.

*Remarks:* Robertson (1978) erected the genus *Boonea*, to which he transferred three western Atlantic species (*Boonea seminuda*, *B. impressa*, and *B. bisuturalis*) from the genus *Odostomia*. The reasons for removing them were valid, and were based on differences (e.g., in protoconch shape, operculum configuration, penial complex, and in the location of the gonoduct aperture) between the *Boonea* species and the *Odostomia* species described by Fretter & Graham (1949).

*Boonea seminuda* (C. B. Adams, 1839)

*Jaminia seminuda* C. B. Adams, 1839: 280, pl. 4 (misnumbered; should be pl. 5), fig. 13; Clench & Turner, 1950: 341, pl. 41, figs. 5–6 (Lectotype: MCZ 186052; type locality): Dartmouth Harbor, Massachusetts).

*Odostomia seminuda* (C. B. Adams, 1839); Gould, 1841: 273; Perry & Schwengel, 1955: 122–123, pl. 23, fig. 164; Andrews, 1971: 129, no figure designation, photo on p. 129; Odé & Spears, 1972: 2, fig. 3; Abbott, 1974: 292, fig. 3487.

*Chemnitzia seminuda* (C. B. Adams); Stimpson, 1851: 11.

*Odostomia (Chrysallida) willisi* Bartsch, 1909: 97, 99, pl. 13, fig. 42.

*Odostomia (Chrysallida) seminuda* Bartsch, 1909: 97, pl. 13, figs. 45, 48.

*Odostomia (Chrysallida) toyatani* Henderson & Bartsch, 1914: 417–418, pl. 13, fig. 2.

*Boonea seminuda* (C. B. Adams, 1839); Robertson, 1978: 364, figs. 3, 10–30.

*Description:* Shell (Fig. 7): Thick, conical, white, 6 mm in length, composed of 4–5 adult whorls. Each whorl with 4 spiral cords parallel to the whorl suture. Cords of upper whorls crossed by perpendicular axial ribs to give a cancellate or latticed appearance. Body whorl 50% of shell length and only upper one-half of spiral cords crossed by axial ribs (Fig. 7A). Intersection of ribs and cords delineate a series of deep, rectangular depressions. Whorl sutures and grooves between spiral cords striated. Auricular aperture ovate, with thick, scalloped outer lip and fluted base. Single, prominent, acute columellar fold on upper half of columella perpendicular to the columella axis (Fig. 7B). Smooth, sinistrally heterostrophic protoconch oriented 120° to teleoconch axis, submerged 40–45% in first adult whorl, with earliest portion of protoconch partially exposed (Fig. 7C–E). Operculum brown, auricular, paucispiral, with subcentric nucleus, but lacking a notch to accommodate columellar fold (Fig. 7F, G).

Head-foot (Fig. 10A): Opaque, lentiginous with scattered white cells (particularly abundant on head posterior to eyes). Anterior portion of foot with slight medial indentation and rounded lateral edges. Foot narrowing posterior to propodium, then widening to gradually taper to a blunt apex. Pedal gland opening at anterior ends of medial groove on ventral surface of foot. Attach-

ment thread present. Tentacles subtriangular, connate, ventro-laterally folded; tentacular pads present. Black eyes beneath epithelium on median side of tentacles. Mentum unnotched, not bifurcate (Fig. 11A). Digestive tissue cells of the visceral mass light brown (with black flecks), yellow to light orange (with brown flecks), or light grey (with black flecks). Reproductive organs opaque to transparent.

Alimentary tract (Fig. 8B): In the retracted condition, the introvert-proboscis extends posteriorly from its aperture on the ventral side of the head, dorsal to the mentum base to enter the cephalic hemocoel. Introvert joining buccal sac, which is connected to buccal pump. Buccal pump divided into anterior (bp1) and posterior sections (bp2), with bp1 one and one-half times longer than bp2; bp1 narrow, round in cross-section, thickened along the last one-third of its length; bp2 wider, laterally flattened, distally rounded. Long, coiled esophagus, with irregular surface, originating on the ventral surface of the alimentary tract at bp1-bp2 juncture, extending into visceral mass and joining stomach. Convoluted salivary gland ducts penetrating alimentary tract immediately anterior to bp1-bp2 juncture, extending parallel to one another within the walls of bp1, and entering stylet bulb without exiting gut. Salivary glands not attached distally to esophagus.

Pallial cavity (Fig. 1A): Mantle and mantle organs typical for members of Odostominae. Mantle edge finely crenulate. Ventral and dorsal ciliated strips joining on mantle roof at posterior end of mantle cavity. Small, oblong pigmented mantle organ composed primarily of cells filled with bright yellow exudate and a few cells containing clear, brown, and green contents; exudate released when snail is disturbed (Table 5). Small pink, white, or light orange ventral ciliated strip gland underlying 20–25% of the ventral ciliated strip. Gill absent.

Reproductive system: Typical of pyramidellids examined (Fig. 5B). Penis in pocket outside and ventral to nerve ring (Fig. 12A). Penis with small, rounded anterior end, narrowing, then widening to become large and bulbous posteriorly. Penis attached anteriorly and posteriorly to floor of its pocket by muscle fibers. Anterior penial opening extending posteriorly into a cavity framed by a single layer of heavily ciliated cuboidal cells. In some specimens, this cavity filled with a brown, glandular substance. Penis opening

to outside via a medial aperture beneath mentum. Producing uncuticularized spermatophores attached to right posterior section of neck prior to exchange with a mate (Robertson, 1978).

Nervous system: Typical for known pyramidellids (Fig. 6A).

*Ecology and Distribution:* *Boonea seminuda* occurs from Prince Edward Island, Canada, south to Florida and Texas (Robertson, 1978) and has several different hosts within its range (Robertson, 1978; Robertson & Mau-Lastovicka, 1979). This species is known to spawn from mid-June to early October in Massachusetts and early July and August in North Carolina (Robertson, 1978). Egg masses have also been found in North Carolina coastal waters in January (Wells & Wells, 1961).

*Boonea cincta* (Carpenter, 1864)

*Chrysallida cincta* Carpenter, 1864: 659, no fig. (Holotype: USNM 15730, type locality: Santa Barbara, California).

*Odostomia (Chrysallida) cincta* (Carpenter); Dall & Bartsch, 1909: 152–153, pl. 15: fig. 2, 2a; Abbott, 1974: 293 fig. 3495; LaFollette 1977: 19, 21, 22, figs. 1–4.

*Odostomia (Chrysallida) vicola* Dall & Bartsch, 1909: 153, pl. 16, fig. 11 (Holotype: USNM 206899; type locality: San Pedro Bay, California).

*Odostomia (Chrysallida) hipolitensis* Dall & Bartsch, 1909: 155, pl. 16, fig. 8 (Holotype: USNM 162770; type locality: Punta San Hipólito, Baja California Sur).

*Odostomia (Chrysallida) pulcia* Dall & Bartsch, 1909: 160, pl. 16, figs. 10–10a (Holotype: USNM 1627630; type locality: San Pedro, California).

*Odostomia (Chrysallida) promeces* Dall & Bartsch, 1909: 164, pl. 18, fig. 2 (Holotype: USNM 162777; type locality: Bahía Todos Santos, Baja California).

*Odostomia (Chrysallida) pulcherrima* Dall & Bartsch, 1909: 164, pl. 17, fig. 7 (Holotype: USNM 206900; type locality: Terminal Island, California).

*Odostomia (Chrysallida) vincta* Dall & Bartsch, 1909: 165, pl. 17, fig. 4 (Holotype: USNM 162726; type locality: San Pedro, California).

*Odostomia (Chrysallida) santorium* Dall & Bartsch, 1909: 167, pl. 18, fig. 1 (Holotype: USNM 46499; type locality: Punta San Hipólito, Baja California Sur).

*Odostomia (Chrysallida) sapia* Dall & Bartsch, 1909: 167, pl. 18, figs. 3, 3a (Holotype: USNM 162775; type locality San Diego, California).

*Odostomia (Chrysallida) deceptrix* Dall & Bartsch, 1909: 169, pl. 17, fig. 1 (Holotype: USNM 206904; type locality: Punta Abrejos, Baja California Sur).

*Odostomia (Chrysallida) contrerasi* Baker, Hanna & Strong, 1928: 231, pl. 12, fig. 13 (Holotype: CASIZ 066090; type locality: "Gulf of California").

*Remarks:* I examined the holotypes of *B. cincta* and all of its synonyms listed above and determined that they are all conspecific. This decision was based on the work of LaFollette (1977), who showed that the shell sculpture of *C. cincta* can be smooth or cancellate, as exemplified by the sculpture of the forms named *Odostomia santorium* and *O. promeces* respectively.

*Boonea cincta*, formerly *Chrysallida cincta*, is anatomically very similar to *Boonea seminuda* the type species of the genus. I have not examined *Chrysallida torrita*, the type species of *Chrysallida*; therefore, it is not possible to determine if *Boonea* is a synonym of the older name *Chrysallida*.

*Description:* Shell (Fig. 9): Thick, conical, white, 4 mm in length, composed of 3–4 adult whorls. Upper whorls with 4 spiral cords parallel to suture. Upper 3 cords crossed by perpendicular axial ribs to give a cancellate or latticed appearance, while fourth cord is smooth (Fig. 9A, C). Body whorl 50% of shell length, with only upper one-half of spiral cords crossed by axial ribs (Fig. 9A). Intersection of ribs and cords delineate a series of deep rectangular depressions. Whorl sutures and grooves between spiral cords striated. Auricular aperture ovate, with thick, scalloped outer lip. Single, prominent, acute columellar fold on upper half of the columella, perpendicular to the columella axis. Protoconch smooth, dextrally heterostrophic, oriented 130° to teleoconch axis, submerged 30–35% in first adult whorl, with earliest portion of protoconch completely submerged (Fig. 9B–E). Operculum, brown, auricular, paucispiral, with subcentric nucleus, but lacking a notch to accommodate columellar fold (Figs. 9F, G).

Head-foot: Opaque with scattered white cells. Anterior portion of foot (= propodium) with slight medial indentation and rounded lateral edges. Foot narrowing posterior to

propodium, then widening to gradually taper to a blunt posterior apex. Pedal gland opening at posterior end of ventral surface of foot. Attachment thread present. Tentacles subtriangular, ventro-laterally folded, joining anteriorly across midline (= connate); tentacular pads present. Black eyes beneath epithelium on median side of tentacles. Mentum unnotched, not bifurcate (Fig. 11A). Visceral mass of yellow and orange (with flecks of brown) digestive tissue cells, translucent to transparent reproductive organs.

Alimentary tract (Fig. 8A): Retracted introvert-proboscis extending posteriorly from its aperture on the ventral side of the head, dorsal to the mentum base and entering cephalic hemocoel. Introvert joining the buccal sac, which is connected to buccal pump. Buccal pump divided into anterior (bp1) and posterior sections (bp2) of equal length; bp1 narrow, round in cross-section; bp2 wider, laterally flattened, distally rounded. Esophagus originating on ventral surface of alimentary tract at bp1-bp2 juncture, extending into the visceral mass, where it joins the stomach. Esophagus long, coiled, with an irregular or tuberculate surface. Salivary gland ducts penetrating alimentary tract immediately anterior to bp1-bp2 juncture, extending parallel to one another within its walls, entering stylet bulb without exiting gut. Salivary glands not attached distally to alimentary tract.

Pallial cavity (Fig. 1A): Mantle and mantle organs typical for members of the Odostominae. Mantle edge finely crenulate. Ventral and dorsal ciliated strips joining on mantle roof at posterior end of mantle cavity. Small, oblong pigmented mantle organ composed primarily of cells filled with bright yellow exudate and a few cells containing brown, orange, or red contents; exudate released when the snail is disturbed (Table 5). Small, cream-colored gland beneath ventral ciliated strip extending posteriorly from anterior edge of ventral ciliated strip to 20–25% of strip's length. Gill absent.

Reproductive system: Typical of pyramidellids examined in this study (Fig. 5B). Penial complex unknown. Egg masses contain approximately 25–35 eggs laid in irregular gelatinous mass on host.

Nervous system: Typical of known pyramidellids (Fig. 6A).

*Ecology and Distribution:* *Boonea cincta* is a common eastern Pacific species, occurring from Santa Barbara to the Gulf of California.



It parasitizes a number of gastropods (e.g., *Norrisia norrisi*, *Astraea undosa*, and *A. gibberosa*; LaFollette, 1977) and can often be found on the dorsal surface of the operculum of the trochid *Tegula eiseni* (LaFollette, 1977; this study). This species' shell was first described based on a single, probably immature, specimen collected at Santa Barbara, California (Carpenter, 1864). The shell sculpture of *B. cincta* varies from highly cancellate to almost entirely smooth (LaFollette, 1977). Living snails collected for this study were all cancellate. This species undergoes direct development (veliger stage at approximately ten days within the cocoon) with juveniles leaving the egg mass at about 27 days (LaFollette, 1979).

#### Genus *Odostomia* Fleming, 1813

*Odostomia* Fleming, 1813: 76. Type-species: *Turbo plicata* Montagu, 1803, by original designation.

**Diagnosis:** Shell white or yellowish, short, conical, 3–5 mm in length, with 4–6 adult whorls. Whorls smooth to cancellate. Body whorl 50–60% of shell length. Umbilicus small or absent. Protoconch smooth, dextrally or sinistrally heterostrophic oriented 120–150° to teleoconch, partially submerged in first adult whorl. Aperture ovate, with single acute columella fold. Operculum brown, ovate, paucispiral, with subcentric nucleus. Head-foot white, with numerous opaque white cells (especially on tentacles and sides of head). Foot narrowing posterior to propodium, widening and then becoming attenuate posteriorly. Pedal gland producing attachment thread. Tentacles subtriangular, connate, ventro-laterally folded; tentacular pads present. Eyes subepithelial on median side of tentacles. Mentum unnotched, not bifurcate. Introvert-proboscis aperture on ventral side of head, dorsal to mentum base. Introvert joining buccal sac, which is composed of sucker, mouth, sheathed stylet with separate opening, oral tube, and stylet bulb. Buccal sac joining buccal pump, which is divided into anterior (bp1) and posterior sections (bp2). Esophagus originating on ventral surface of bp1-bp2 juncture. Salivary gland ducts entering alimentary tract and extending parallel to one another within walls of bp1. Just posterior to buccal sac, ducts exiting alimentary tract and entering stylet bulb.

**Remarks:** The genus *Odostomia* is one of four genera recognized by Dall & Bartsch (1904, 1909) to which they assigned 40 subgenera on the basis of a small number of convergent shell characters (Abbott, 1974).

*Odostomia babylonica* (C. B. Adams, 1845)

*Chemnitzia babylonica* C. B. Adams, 1845: 6; Clench & Turner, 1950: 259 (type lost, fide Clench & Turner; type locality: Jamaica).

*Odostomia (Cingulina) babylonica* [sic] (C. B. Adams); Bush, 1899: 176.

*Odostomia (Cingulina) babylonica* [sic] (C. B. Adams); Verrill & Bush, 1900: 534, pl. 65, fig. 11.

*Odostomia (Miralda) judithae* Usticke, 1959: 86–87, pl. 4, fig. 16, (Holotype: AMNH 198476, type locality: Sugar Bay, St. Croix, U. S. Virgin Islands).

*Cingulina judithae* (Usticke); Usticke, 1969: 31.

*Pyramidelloides judithae* (Usticke); Usticke, 1971: 28.

*Cingulina babylonica* (C. B. Adams); Abbott, 1974: 301; DeJong & Coomans, 1988: 120, pl. 19, fig. 637.

*Liamorpha babylonica* (C. B. Adams); Faber, 1988: 81.

**Remarks:** Abbott (1974: 301), DeJong & Coomans (1988: 20) and Faber (1988: 81) all considered *Odostomia judithae* Usticke to be a junior synonym of *O. babylonica* C. B. Adams. Although Adams' type material is lost, his description of this highly sculptured species is unmistakable. Moreover, this species was accurately figured by Verrill & Bush (1900).

**Description:** Shell (Fig. 13): Polished, transparent, conical, 2 mm in length, composed of 3–4 adult whorls (Fig. 13A). Whorls posterior to body whorl with two strong spiral cords: one subsutural (a part of the shoulder at each suture) and one equally dividing each whorl. Numerous, irregular ridges perpendicular to shoulder edge and often extending to the suture (Fig. 13B). Body whorl 50% of shell length. Each whorl with tightly spaced, layered, nearly orthocline growth lines that are crossed by numerous microscopic spiral lines (Fig. 13B). Aperture ovate, thick, ribbed at outer lip. Single, prominent, acute columellar fold on upper half of the columella, perpen-

dicular to columella axis. Protoconch smooth, sinistrally heterostrophic, oriented  $120^\circ$  to teleoconch, submerged 30–35% in first adult whorl, with earliest portion of protoconch partially exposed (Fig. 13C–E). Operculum light brown, lenticular, paucispiral, with a subcentric nucleus. Operculum lacking notch to accommodate columellar fold (Fig. 13F, G).

Head-foot (Fig. 10B): White and opaque to translucent. Anterior portion of foot with slight medial indentation and rounded antero-lateral edges. Foot narrowing posterior to propodium, widening, becoming posteriorly attenuate. Pedal gland opening medially on posterior end of ventral surface of foot. Attachment thread present. Aggregate of large, white subepithelial cells lying just anterior to operculum. Tentacles subtriangular, connate, ventro-laterally folded; tentacular pads present. Eyes black, large, round, subepidermal close together on median side of tentacles. Mentum unnotched attached to foot laterally, not bifurcate (Fig. 11B). Visceral mass of pale orange, light brown, dark blue, or burgundy digestive tissue cells and opaque reproductive organs.

Alimentary tract (Fig. 8C): Retracted introvert-proboscis extending posteriorly from its aperture on the ventral side of the head, dorsal to the mentum base and entering the cephalic hemocoel. Introvert joining buccal sac, which is connected to buccal pump. Buccal pump is divided into anterior (bp1) and posterior sections (bp2); bp1 elongate spherical; bp2 one and one-half times length of bp1, wider, oblong, circular in cross-section. Esophagus originating on the ventral surface of alimentary tract at bp1-bp2 junction, extending into the visceral mass to join stomach. Esophagus long, coiled, with a tuberculate surface. Short, uncoiled salivary gland ducts penetrating alimentary tract at the distal end of bp1. Ducts extending parallel to one another within the walls of bp1, exiting the alimentary tract immediately posterior to buccal sac and entering stylet bulb. Salivary glands not attached distally to alimentary tract.

Pallial cavity (Fig. 1A): Mantle and mantle organs as in other *Odostominae*. Mantle edge finely crenulate. Ventral and dorsal ciliated strips joining on mantle roof at posterior end of mantle cavity. Small, oblong pigmented mantle organ composed primarily of large cells containing bright yellow exudate and a few cells filled with brown, red, or black contents; exudate released when the snail is

disturbed (Table 5). Cream-colored, ventral ciliated strip gland extending posteriorly from beneath the anterior edge of the ventral ciliated strip to 20–25% of the strip's length. Gill absent.

Reproductive system: Typical of pyramidellids examined this study (Fig. 5B). Penial complex unknown.

Nervous system: Typical of known pyramidellids (Fig. 6A).

*Ecology and Distribution:* *Odostomia babylo-nia* is found littorally to just sublittorally, inhabiting the underside of embedded rocks and coral rubble, from West Indies (Abbott, 1974: 301). Host unknown.

*Odostomia didyma* Verrill & Bush, 1900

*Odostomia (Cyclodostomia) didyma* Verrill & Bush, 1900: 533, pl. 65, fig. 14. (Holotype: PM 15706; type locality: Bermuda). *Odostomia didyma* Verrill & Bush; DeJong & Coomans, 1988: 122, pl. 19, fig. 641.

*Description:* Shell (Fig. 14): Vitreous, thick, conic, 2 mm in length, composed of 3–4 adult whorls. Whorls with thick spiral cord just above suture. Sloping subsutural shelf ventral to each suture (Fig. 14C). Body whorl 50% of shell length. Entire shell etched by microscopic prosocline growth lines. Aperture rhomboid with thick, basally flared outer lip. Single, prominent, acute columellar fold on upper half of the columella, perpendicular to columella axis. Protoconch smooth, dextrally heterostrophic, oriented  $130^\circ$  to teleoconch, submerged 30–35% in first adult whorl, with earliest portion of protoconch completely submerged (Fig. 14B–E). Operculum light brown, lenticular, paucispiral, with subcentric nucleus. Operculum lacking notch to accommodate columellar fold (Figs. 14F, G).

Head-foot (Fig. 10C): Transparent to opaque. Golden-yellow pigmentation present on dorsal periphery of foot, mantle floor parallel to dorsal ventral ciliated strip, and the length of tentacles laterally. White cells, although scattered around head-foot, concentrated just posterior to eyes. Anterior portion of foot with sharp antero-lateral projections and deep medial indentation. Foot constricting immediately behind propodium, widening, narrowing again and tapering to a blunt posterior apex. Pedal gland opening in middle of a groove extending along the posterior

half of ventral surface of the foot. Attachment thread present. Tentacles long, subtriangular, connate, ventro-laterally folded; tentacular pads present. Eyes black, subepithelial, bean-shaped lying close together on median side of tentacles. Mentum very short, unnotched, not bifurcate, with lateral attachments nearly even with its anterior edge (Fig. 11C). Visceral mass composed of brown, grey, black, or burgundy digestive tissue cells and opaque reproductive organs.

Alimentary tract (Fig. 8D): Retracted introvert-proboscis extending posteriorly from its aperture on the ventral side of the head, dorsal to the mentum base to enter cephalic hemocoel. Introvert joining buccal sac, which is connected to buccal pump. Buccal pump divided into anterior (bp1) and posterior sections (bp2); bp1 elongate, spherical; bp2 one and one-half times length of the bp1, wider, oblong, circular in cross-section. Esophagus originating on alimentary tract at juncture of bp1-bp2, and extending posteriorly to join the stomach within the visceral mass. Esophagus long, coiled, with irregular surface. Salivary gland ducts penetrating alimentary tract at distal end of bp1, continuing anteriorly and parallel to one another within the walls of the bp1, entering the stylet bulb without exiting alimentary tract. Salivary glands not attached distally to alimentary tract.

Pallial cavity (Fig. 1A): Mantle and mantle organs as in other *Odostominae*. Mantle edge finely crenulate. Ventral and dorsal ciliated strips joining on mantle roof at posterior end of mantle cavity. Small, oblong pigmented mantle organ composed primarily of dark and variably colored cells filled with a combination of: (a) yellow, black, red, and orange, (b) yellow and dark brown, or (c) yellow, brown, red or black contents. Snail exuding a large amount of bright yellow exudate when disturbed (Table 5). Cream-colored gland beneath ventral ciliated strip extending posteriorly from the strip's anterior edge to 20–25% its length. Gill absent.

Reproductive system: Typical of pyramidellids in this study (Fig. 5B). Penial complex unknown. Producing cuticularized spermatophores, that, while commonly attached by their bulbous end to the parietal wall of the shell, were also seen attached to operculum and immediately inside the shell's aperture. Fresh spermatophores golden-brown.

Nervous system: Characteristic of known pyramidellids (Fig. 6A).

*Ecology and Distribution:* *Odostomia didyma* is found intertidally to subtidally on the underside of embedded rocks and coral rubble, from Bermuda to Curaçao, Netherlands Antilles (Dejong & Coomans, 1988). Host unknown.

### Subfamily Sayellinae, new subfamily

*Genus Sayella* Dall, 1885

*Sayella* Dall, 1885: 286. Type-species: *Leuconia hemphillii* Dall, 1884, by original designation.

*Diagnosis:* Shell brown, pupoid to elongate-pupoid, with subsutural white band, 4–5 mm in length, with 4–5 adult whorls. Sides of whorls convex to straight. Body whorl 40–50% of shell length. Umbilicus absent. Protoconch smooth, dextrally heterostrophic, partially submerged in first adult whorl, oriented 140° to teleoconch. Aperture auricular, with single columellar fold originating basally on columella, extending at an oblique angle to upper half of the columella. Operculum light brown, lenticular, with subcentric nucleus. Head-foot and mantle darkly pigmented. Foot broad anteriorly, tapering posteriorly to blunt point. Attachment thread absent. Tentacles stout, cylindrical, not connate; tentacular pads absent. Eyes black subepithelial, on median side of tentacles. Mentum emarginate, short, with shallow longitudinal medial cleft. Introvert-proboscis aperture medial at anterior mentum tip. Introvert joining buccal sac posteriorly; buccal sac composed of sucker, sheathed stylet, mouth-stylet aperture, and stylet bulb. Buccal sac extending posteriorly to join buccal pump, which is divided into anterior (bp1) and posterior sections (bp2). Anterior esophagus originating at ventral surface of buccal pump, continuing posteriorly to join posterior esophagus and paired salivary glands, forming a four-way junction. Salivary gland ducts attached to exterior of esophagus. Anterior to anterior esophagus-buccal pump junction, ducts detached and entering stylet bulb. Salivary glands attached distally to alimentary tract. Anteriorly tapered, hooded penis outside and ventral to nerve ring.

*Remarks:* Dall (1883) originally believed *S. hemphillii* to be a freshwater ellobiid and assigned it to the genus *Leuconia*. Later, Dall (1885) placed this species and *S. crosseana*

(Dall, 1885) in his new subgenus *Sayella* within the genus *Melampus* Montfort, 1810. Subsequently, *Sayella* was transferred to the Pyramidellidae by Morrison (1939) based on his study of *S. chesapeakea* Morrison, 1939.

*Sayella hemphillii* (Dall, 1884)

*Leuconia hemphillii* Dall, 1884: 323, pl. 10, fig. 6. (Holotype: USNM 36016; type locality: Cedar Key, Florida).

*Melampus (Sayella) hemphillii* (Dall); Dall, 1885: 286, pl. 18, fig. 11.

*Sayella livida* Rehder, 1935: 129, pl. 7, fig. 7; Abbott, 1974: 300, fig. 3649 (Holotype: USNM 125556; type locality: Corpus Christi Bay, Texas); Harry, 1984: 68–70, 72, 74.

*Odostomia (Syrnola) cf. livida* Rehder, 1935; Andrews, 1977: 127–128, unnumbered fig.

*Synonymic Remarks:* Rehder (1935) noted that the shells of *S. livida* and *S. hemphillii* are very similar and suggested that examination of more specimens may show that the two are conspecific. Examination of the *S. livida* holotype and material collected in Florida indicates that they are, in fact, the same species.

*Description:* Shell (Fig. 15): Elongate pupoid (Fig. 15A) to pupoid (Fig. 15B), dark red-brown, with whitish subsutural band at each whorl, 4–5 mm in length, composed of 4–5 convex whorls. Adult whorls with numerous microscopic, orthocline growth lines (Fig. 15D). Sutures shallow, simple. Body whorls 40–50% of shell length. In older individuals, upper whorls and protoconch etched, pitted or extensively eroded (Fig. 15A). Aperture ovate in young specimens, elongate-ovate in mature snails. Single columellar fold originating at base of columella, extending at an oblique angle to upper half of columella (Fig. 15C). Protoconch smooth, dextrally heterostrophic, oriented 140° to teleoconch, submerged 50–55% in adult shell, with earliest portion of protoconch completely submerged (Fig. 15D, E). Operculum light brown, lenticular, with subcentric nucleus (Fig. 15G, H), lacking notch to accommodate columellar fold.

Head-foot (Fig. 16A): Generally heavily pigmented giving snail a “sooty” appearance (although a few snails were only lightly pigmented). White to opaque cells between eyes and scattered throughout dorsal surface of

foot. Anterior edge of foot convex, with slight rounded lateral projections. Foot narrowing posterior to propodium, widening, ending in bluntly attenuated tip. Attachment thread absent. Tentacles cylindrical, stout, not connate; tentacular pads absent. Eyes black, subepithelial, round, on median side of tentacles. Mentum emarginate, short, anteriorly rounded, with shallow longitudinal medial cleft (Fig. 11H). Visceral mass composed of grey, black, or light brown digestive tissue cells and transparent to translucent reproductive structures.

Alimentary tract (Fig. 17A): Retracted introvert-proboscis extending posteriorly from its medial aperture at the anterior mentum tip to enter the cephalic hemocoel and join the buccal sac. Buccal sac continuing posteriorly to buccal pump, which is divided into anterior (bp1) and posterior sections (bp2); bp1 two times the length of the laterally flattened bp2. Anterior esophagus originating on ventral surface of alimentary tract at bp1-bp2 junction. Anterior esophagus joining posterior esophagus and paired salivary glands to form a four-way junction. Posterior esophagus widening posterior to four-way junction and extending into visceral mass to join the stomach. Salivary gland ducts arranged in tight folds affixed to exterior of anterior esophagus, extending anteriorly, leaving anterior esophagus at esophagus-buccal pump junction, straightening and entering stylet bulb. Salivary glands attached distally to alimentary tract at posterior esophagus.

Pallial cavity (Fig. 1A, C): Mantle and mantle organs typical for pyramidellids. Mantle edge scalloped. Iridescent ventral and dorsal ciliated strips joining on the mantle roof at posterior end of mantle cavity. Small, oblong pigmented mantle organ composed primarily of transparent and white cells, with a few scattered cells filled with red, yellow, and orange contents (Fig. 1A). Pigmented mantle organ producing no exudate. Gland beneath ventral ciliated strip underlying entire ventral ciliated strip, darkly pigmented, with a few scattered red cells, producing and exuding copious milky-blue exudate (Table 5). Cream-colored kidney visible through transparent dorsal pallial roof, because the mantle area above this organ unpigmented. Gill absent.

Reproductive system: Typical of pyramidellids in this study (Fig. 5B). Penis within head just anterior and ventral to nerve ring (Fig. 12B). Penis in a pocket that opens me-

dially and ventral to mentum base. Elongate anterior section of penis cylindrical, with a subapical swelling that narrows to form a short terminal nipple. Anterior portion framed posteriorly by large, pleated fleshy hood that contains numerous glandular cells. Penis anchored to pocket posteriorly and at base of hood by muscle and connective tissue.

Nervous system: Typical for known pyramidellids (Fig. 6A).

*Ecology and Distribution:* *Sayella hemphillii* occurs intertidally to subtidal in the surface layers of sand and mud flats in the Gulf of Mexico along the coast Texas and west Florida (Abbott, 1974). In this study, *S. hemphillii* were collected at Cedar Key, Florida, in areas with large concentrations of the polychaete *Onuphis magna*, which is a possible host.

### Genus *Petitella*, new genus

Type-species: *Melampus (Sayella) crosseana* Dall, 1885: 286, here designated.

*Diagnosis:* Shell pupoid to elongate pupoid, semitransparent and yellow brown around lower periphery of body whorl, 3–4 mm in length, composed of 4–5 straight to slightly convex adult whorls. Whorls with numerous, nearly orthocline microscopic growth lines. Body whorl 50% of shell length. Protoconch smooth, dextrally heterostrophic, submerged 50–55% in first adult whorl, oriented 140–145° to teleoconch, with earliest portion of protoconch completely submerged. Aperture elongate-ovate, with thin outer lip slightly flared basally. Single, columella fold originating at base of columella, extending obliquely to upper half of the columella. Parietal wall dark golden-brown. Operculum tan, auricular, with subcentric nucleus. Head-foot opaque to transparent, with white cells concentrated at mentum. Foot with broad anterior and slightly convex rounded lateral edges, tapering posteriorly to blunt apex. Attachment thread absent. Tentacles stubby, cylindrical, rounded apically, not connate; tentacular pads absent. Eyes black subepithelial, spherical, on median side of tentacles. Mentum emarginate, antero-laterally rounded with medial longitudinal cleft. Introvert-proboscis aperture at anterior tip of mentum. Introvert joining buccal sac, which is composed of sucker, sheathed stylet, mouth/stylet aperture, and stylet bulb. Long, undifferentiated buccal pump posterior to buccal sac. Buccal pump without blind sac

or caecum. Esophagus extending posteriorly, entering visceral mass and joining stomach. Salivary gland ducts penetrating alimentary tract at stylet bulb. Salivary glands attached distally to alimentary tract at anterior portion of esophagus. Retracted penis folded within pocket that opens ventro-medially to mentum outside and ventral to the nerve ring.

*Petitella crosseana* (Dall, 1885)

*Melampus (Sayella) crosseana* Dall, 1885: 286, pl. 18, fig. 10. (Holotype: USNM 37613; type locality: Egmont Key, Florida).

*Sayella crosseana* (Dall); Abbott, 1974: 300.

*Remarks:* *Petitella crosseana* was originally assigned to the genus *Sayella* on the basis of shell characters. Anatomically, *P. crosseana* is unlike any known sayellids (e.g., *Sayella hemphillii*) or for that matter any known pyramidellids. Consequently, I propose that it be placed in a new genus. Etymology: *Petitella* is named for Richard E. Petit in recognition of his contributions to malacology.

*Description:* Shell (Fig. 18): Polished, semitransparent, pupoid to elongate pupoid, yellow brown around lower periphery of body whorl (Fig. 18A), 3–4 mm in length, composed of 4–5 straight to slightly convex adult whorls. Whorls with numerous, nearly orthocline microscopic growth lines (Figs. 18B, C). Body whorl 50% of shell length. Upper adult whorls and protoconch often eroded and pitted. Aperture elongate-ovate, with thin outer lip slightly flared basally. Single, columella fold originating at base of columella, extending obliquely to upper half of columella. Parietal wall dark golden-brown. Protoconch smooth, dextrally heterostrophic, submerged 50–55% in first adult whorl, oriented 140–145° to teleoconch, with earliest portion of protoconch completely submerged (Fig. 18C–E). Operculum tan, auricular, with subcentric nucleus (Fig. 18F, G).

Head-foot (16B): Opaque to transparent, with white cells concentrated at mentum. Anterior portion of short foot broad, slightly convex, with rounded lateral edges. Foot tapering posteriorly to blunt apex. Attachment thread absent. Tentacles cylindrical, stubby, rounded apically, not connate; tentacular pads absent. Eyes black, subepithelial, spherical, on median side of tentacles. Men-

tum emarginate, antero-laterally rounded, with medial longitudinal cleft (Fig. 11I). Visceral mass of white-opaque reproductive organs and a distinctive branching network of brown to black digestive tissue cells, this network generally arranged perpendicular to the coiling axis of the visceral mass and visible through shell.

Alimentary tract (Fig. 17B): When retracted, introvert-proboscis extending posteriorly from its medial aperture at anterior tip of mentum to enter cephalic hemocoel and join buccal sac. Long, undifferentiated muscular conduit posterior to buccal sac functioning as buccal pump. Buccal pump without blind sac or caecum. Esophagus extending posteriorly, entering the visceral mass and joining stomach. Salivary gland ducts penetrating alimentary tract at stylet bulb. Salivary glands attached distally to alimentary tract at anterior portion of esophagus.

Pallial cavity (Fig. 1A, C): Mantle and mantle organs as in other pyramidellids. Mantle edge finely scalloped. Small, oblong, pigmented mantle organ containing either large cells filled with a bright yellow exudate and a few cells containing orange contents, or cells with black contents and a small number of cells filled with a white exudate. Pigmented mantle organ secreting a light blue exudate when snail disturbed (Table 5). Gland beneath ventral ciliated strip composed mostly of large white cells mixed with a few black cells, extending the length of the ventral ciliated strip. Gill absent.

Reproductive system: Typical of pyramidellids herein (Fig. 5B). Penis outside and ventral to the nerve ring. Retracted penis folded within a pocket that opens ventro-medially to mentum (Fig. 12C). Posterior end anchored to floor of pocket by several retractor muscles. Penis anteriorly attenuate, posteriorly bulbous. Shallow dorsal groove extends posteriorly from penis anterior to one-half penis length.

Nervous system: Characteristic of known pyramidellids (Fig. 6A).

*Ecology and Distribution:* *Petitella crosseana* occurs intertidally to subtidally in the surface layers of mud and sand flats in the Gulf of Mexico along the coast of Texas and west Florida (Abbott, 1974), and in the Atlantic, South Carolina (Merrill & Petit, 1965) to Florida (present study), south to the West Indies (Abbott, 1974). Host unknown.

Subfamily Pyramidellinae Gray, 1840

Genus *Pyramidella* Lamarck, 1799

*Obeliscus* Humphrey, 1797: 24. [Rejected work, I.C.Z.N. Opinion 51].

*Pyramidella* Lamarck, 1799: 76. Type-species: *Trochus dolabratus* Linnaeus, 1758, by monotypy.

*Pyramidellus* Montfort, 1810: 499. Type species: *Trochus dolabratus* Linnaeus, 1758, by monotypy.

*Aphalista* Laseron, 1959: 1876. Type species: *Pyramidella mitralis* A. Adams, 1853, by original designation.

*Diagnosis:* Shell elongate-conical, porcellaneous, generally white or brown, with or without bands or spots, reaching 50 mm in length. Sides of whorls convex to straight. Body whorl approximately 40% of shell length. Umbilicus present. Protoconch smooth, sinistrally heterostrophic protoconch oriented 120–125° to teleoconch, partially submerged in first adult whorl. Aperture elongate-ovate, with one large and two smaller prominent columellar folds. Operculum brown, elongate-ovate, notched to accommodate largest columellar fold. Head-foot light yellow, with a prominent mass of white cells between and posterior to eyes. Foot wide anteriorly, with shallow medial indentation and bluntly tapered posterior apex. Attachment thread absent. Tentacles triangular, connate, medially notched, laterally folded; tentacular pads absent. Eyes black, subepithelial on median side of tentacles. Mentum retuse, broad anteriorly, with sharp antero-lateral projections and shallow longitudinal groove. Introvert-proboscis aperture opening medially on mentum tip. Introvert connecting posteriorly to buccal sac, which is composed of sucker, sheathed stylet, mouth-stylet aperture and stylet bulb. Buccal sac joining buccal pump separated into very short anterior section (bp1) and very elongate, laterally flattened posterior section (bp2). Esophagus divided into anterior and posterior sections that, with the salivary glands, form a four-way junction. Salivary gland ducts, attached to exterior of anterior esophagus, extending anteriorly and entering stylet bulb. Salivary glands attached distally to alimentary tract at posterior esophagus. Ciliated, scoop-shaped penis, with bulbous posterior end outside and ventral to nerve ring.

*Remarks:* The genus *Pyramidella* was first proposed by Lamarck in 1799. Historically, confusion has existed over the use of *Pyra-*

*midella* because the genus *Obeliscus* was often used in its place in the older literature. However, the name *Obeliscus* is no longer considered available because it was proposed by Humphrey (1797), a work rejected for nomenclatural purposes (I.C.Z.N. Opinion 51).

*Pyramidella sulcata* (A. Adams, 1854)

*Obeliscus sulcatus* A. Adams, 1854: 807, pl. 171, fig. 34. (Holotype: BMNH 1986: 284; type locality: Tahiti).

*Obeliscus monilis* A. Adams, 1854: 806, pl. 171, fig. 12.

*Obeliscus teres* A. Adams, 1854: 807, pl. 171, figs. 31, 32.

*Obeliscus tessellatus* A. Adams, 1854: 808, pl. 171, fig. 16.

*Pyramidella pratii* Bernardi, 1859: 386, pl. 13, fig. 1.

*Pyramidella teres* (A. Adams); Sowerby, 1865: pl. 1, fig. 6.

*Pyramidella tessellatus* (A. Adams); Sowerby, 1865: pl. 1, fig. 4.

*Pyramidella sulcata* (A. Adams); Tryon, 1886: 301, pl. 72, figs. 79–83; Cernohorsky, 1972: 200, pl. 57, fig. 2, 2a; Kay, 1979: 413, fig. 133B.

*Wingenella pricensa* Laseron, 1959: 190–191, figs. 17, 18.

*Wingenella eburnea* Laseron, 1959: 190, figs. 14–16.

**Synonymic Remarks:** The nominal species *Obeliscus teres* A. Adams, *O. tessellatus* A. Adams, *O. monilis* A. Adams, were named at the same time as *O. sulcata* A. Adams. Tryon (1886: 301) considered the four to be conspecific and acted as first reviser in selecting *O. sulcatus* as the senior synonym. *Pyramidella pratii* Bernardi, *Wingenella eburnea* Laseron, and *W. pricensa* Laseron are also considered conspecific (Cernohorsky, 1972: 200).

**Description:** Shell (Fig. 19): White, polished, elongate-conical, with orange-brown squarish spots, 20–30 mm in length, composed of 12–13 adult whorls. Sides of whorls convex to straight, with microscopic orthocone growth lines (Fig. 19B). Sutures deeply channeled. Body whorl 40% of shell length. Upper whorls and protoconch, often eroded and pitted (Fig. 19F, H). Aperture elongate-ovate, with thin outer lip and thick columella. One large columellar fold on upper half of columella dorsal

to two smaller folds (Fig. 19C). Columellar folds perpendicular to the columella axis. Largest columellar fold with four well-developed ridges composed of overlapping imbricate plates (Fig. 19D, E); ridges partially worn or highly eroded (resorbed?) in the whorls above the penultimate whorl (= whorl preceding body whorl). The two smaller columellar folds smooth. Six to eight well-developed palatal teeth present deep inside the aperture of the body whorl (Fig. 19C). Rudimentary palatal teeth in various stages of ontogeny present immediately inside the outer lip in some. Protoconch smooth, sinistrally heterostrophic, oriented 120° to teleoconch, submerged 40–45% in first adult whorl, with earliest portion of protoconch partially exposed (Fig. 19F, H). Operculum light brown, elongate-ovate, notched to fit largest columellar fold (Fig. 19I).

**Head-foot** (Fig. 20A): Light yellow, with prominent clumps of subepithelial, numerous white cells posterior to and between eyes, on tentacles, mentum, and foot, particularly just anterior to operculum. Foot blunt posteriorly, widening anteriorly, narrowing, then widening again at slightly bifid propodium. Propodium with rounded antero-lateral edges. Attachment thread absent. Tentacles triangular, connate, medially notched, laterally folded; tentacular pads absent. Eyes black, subepithelial on median side of tentacles. Mentum retuse, with medial longitudinal groove (Fig. 11D). Columellar muscle divided into three sections. Middle and longest portion, attached to columella within the penultimate whorl, tapering anteriorly and joining four-way junction of alimentary tract. Visceral mass composed of grey, black, brown, or dark red-brown digestive tissue cells and opaque reproductive organs. Visceral mass partially covered in densely packed small white cells.

**Alimentary tract** (Fig. 21A): When retracted, introvert-proboscis extending posteriorly from its medial aperture on the anterior apex of mentum to enter cephalic hemocoel. Introvert entering cephalic hemocoel, forming a tight coil, and joining the buccal sac. Buccal sac joining buccal pump, which is divided into laterally flattened posterior section (bp2), which is 10 times length of anterior section (bp1). Anterior esophagus originating on ventral surface of alimentary tract at juncture of bp1-bp2. Anterior esophagus stretching posteriorly, joining posterior esophagus and paired salivary glands to form four-way junc-

tion. Posterior esophagus narrow at four-way junction, widening posteriorly, extending into visceral mass and joining stomach. Highly folded, tightly packed salivary gland ducts attached to outside of anterior esophagus. Ducts extending from salivary glands to anterior esophagus-buccal pump juncture, then straightening and entering stylet bulb. Salivary glands attached distally to alimentary tract at anterior end of posterior esophagus by connective tissue or muscle. There are two pairs of retractor muscles. The first pair long, extending anteriorly from that portion of muscular enclosure even with the buccal sucker, attaching to the proboscis. The second pair originating further anterior on the proboscis, where first pair terminates and muscular sleeve ends, continuing anteriorly approximately 1 mm and attaching to the proboscis.

Pallial cavity (Fig. 1B): Mantle and mantle organs typical for the Pyramidellinae. Mantle edge smooth. Ventral and dorsal ciliated strips joining on mantle roof at posterior end of mantle cavity. Very large, pigmented mantle organ, composed of transparent and opaque cells, extending posteriorly, narrowing and terminating at convergence of ventral and dorsal ciliated strips. Pigmented mantle organ secreting a very viscid, clear to opaque substance. Large, yellow gland beneath ventral ciliated strip extending posteriorly from anterior edge of ventral strip to strip's terminus. Gland composed primarily of large cells filled with a yellow exudate and a few cells containing red and white contents; bright yellow exudate released when the snail disturbed (Table 5). Osphradium subtriangular, with numerous elliptical white cells, mostly concentrated on extreme left side of mantle roof, narrowing as it extends laterally, terminating just posterior to right mantle edge (Fig. 6B). Small, white gland cells originating at the convergence of dorsal and ventral strips and extending anteriorly atop the middle of the gill to the anterior mantle edge. Gill composed of a series of grooves and ridges perpendicular to and enclosed by opposing ciliated strips (Fig. 4B). Individual gill filaments highly folded (Fig. 4C). Medial section of gill surface with scattered tufts of long cilia, bordered laterally by densely packed shorter cilia.

Reproductive system: Typical of pyramidellids discussed herein (Fig. 5B). Penis in cavity outside and ventral to nerve ring (Fig. 22A). Protrusile penis with sides that fold in-

ward to form a narrow groove that extends length of organ. Grooved and deltoid tip of penis ciliated. Posterior portion of penis composed of bulbous halves containing brown glandular cells. Muscle fibers and connective tissue attached to posterior of penis function as retractors and anchor penis to its enclosure. Penis exiting the body through medial opening ventral to mentum.

Nervous system: As in other pyramidellids (Fig. 6A), with one exception: the osphradial nerve bifurcating to innervate both right and left portions of osphradium (Fig. 6B).

*Ecology and Distribution:* *Pyramidella sulcata* occurs intertidally to subtidally throughout the Indo-Pacific (Cernohorsky, 1972). It remains within the sand during the day and at night is epifaunal (this study). Host unknown.

*Pyramidella crenulata* (Holmes, 1859)

*Pyramidella crenulata* Holmes, 1859: 88, pl. 13, figs. 14, 14a. (Holotype: AMNH 099185; type locality: Pleistocene; South Carolina.

*Pyramidella (Longchaeus) crenulata* (Holmes); Perry & Schwengel, 1955: 118, pl. 23, fig. 154; Andrews, 1977: 127, unnumbered fig.; Abbott, 1974: 291, fig. 3462.

*Obeliscus arenosa* Conrad; Tuomey & Holmes, 1857: pl. 26, fig. 17 (not of Conrad, 1843: 309).

*Description:* Shell (Fig. 23): Polished and elongate-conical, 12–14 mm in length, composed of 10–12 adult whorls. Whorls flat to slightly convex, with moderately deep crenulated sutures (Fig. 23B). Two color forms: (1) solid white and (2) brown with white spots. Body whorl 40% of shell length. Protoconch and upper adult whorls eroded and pitted (Fig. 23A, E). Aperture elongate-ovate, with thick columella and thin outer lip. One large columellar fold on upper half of columella, dorsal to two smaller folds, all folds perpendicular to columella axis (Fig. 23C). Large columellar fold with a single ridge composed of disjunct and/or imbricate plates and bordered by an outer notched edge (Fig. 23D). Smaller columellar folds smooth. Generally with 3–4 fully developed palatal teeth within aperture of body whorl (Fig. 23C). Rudimentary palatals are usually present just inside outer lip. Protoconch smooth, sinistrally heterostrophic, oriented 120° to teleoconch, submerged 40–



45% in first adult whorl, with earliest portion of protoconch partially exposed (Fig. 23E, G). Operculum light brown, elongate-ovate, notched to accommodate largest columellar fold (Fig. 23H, I).

Head-foot (Fig. 20B): White with prominent white cells dispersed throughout but particularly ventral to and surrounding antero-dorsal edge of operculum. Foot blunt posteriorly, wide across midfoot, narrowing at anterior end. Propodium slightly bifid, with rounded antero-lateral edges. Attachment thread absent. Tentacles triangular, connate, medially notched, laterally folded tentacles; tentacular pads absent. Eyes black subepithelial, spherical, on median side of tentacles. Mentum re-use mentum with medial longitudinal groove (Fig. 11D). Columella muscle as in *P. sulcata*. Visceral mass with dark, brown-red digestive cells and opaque to translucent reproductive organs. Visceral mass coils partially covered by numerous densely packed white cells.

Alimentary tract (Fig. 21A): When retracted, introvert-proboscis extending posteriorly from its medial aperture on the anterior mentum tip to enter cephalic hemocoel. Introvert entering cephalic hemocoel twisted into single tight coil, joining buccal sac. Buccal pump as in *P. sulcata*. Short anterior esophagus uniting with buccal pump at juncture of bp-bp2, extending posteriorly, joining posterior esophagus and salivary glands, forming a four-way junction. Posterior esophagus narrow at four-way junction, widening posteriorly prior to entering the visceral mass and joining stomach. Salivary gland ducts affixed to exterior of anterior esophagus. These highly folded ducts extending anteriorly from anterior esophagus-buccal pump junction, entering stylet bulb. Salivary glands attached distally to alimentary tract at anterior portion of posterior esophagus. Retractor muscles as in *P. sulcata*.

Pallial cavity (Fig. 1B): Mantle configuration typical for the Pyramidellinae. Mantle edge smooth. Ventral and dorsal ciliated strips joining on mantle roof at posterior end of mantle cavity. Very large, elongate pigmented mantle organ of clear to translucent cells with a few scattered white cells, releasing a small amount of opaque substance flecked with white. Large, yellow gland beneath ventral ciliated strip extending length of the strip. Gland composed primarily of large cells filled with yellow exudate and a few cells with white and red contents; viscid, bright yellow exudate released when snail disturbed

(Table 5). Osphradium as in *P. sulcata*. Rows of small white and brown cells at the convergence of dorsal and ventral ciliated strips, extending anteriorly atop middle of gill, terminating at anterior edge of mantle floor. Gill as in *P. sulcata*.

Reproductive system: Typical of pyramidellids in this study (Fig. 5B). Penial complex as in *P. sulcata* (Fig. 22A).

Nervous system: As in other taxa within the subfamily Pyramidellinae (Fig. 6A, B).

*Ecology and Distribution:* *Pyramidella crenulata* occurs intertidally to subtidally in sand and mud from North Carolina to Texas and West Indies (Abbott, 1974). As with other members of the subfamily, it is probably epifaunal at night. Host unknown.

*Pyramidella mitralis* A. Adams, 1854

*Pyramidella mitralis* A. Adams, 1854: 814, pl. 172, fig. 9; (Holotype: BMNH 19862799; type locality: St. Estevan, North Ilocos, Isle of Luzon, Philippine Islands); 1855: 177; Sowerby, 1865, pl. 3, species 20.

*Pyramidella propinqua* A. Adams, 1854: 814; pl. 172, fig. 8; 1855:177.

*Pyramidella variegata* A. Adams, 1854: 814, pl. 172, fig. 10; 1855: 178.

*Pyramidella (Otopleura) mitralis* A. Adams; Tryon, 1886: 305, pl. 73, figs. 94, 97, 2, 3.

*Aphalista mitralis* (A. Adams); Laseron, 1959: 187, figs. 4–6.

*Otopleura mitralis* (A. Adams); Cernohorsky, 1972: 201, pl. 57, fig. 6–6C; Kay, 1979: 412, fig. 133C.

*Synonymic Remarks:* *Pyramidella propinqua* A. Adams and *P. variegata* A. Adams are placed in synonymy on the authority of Tryon (1886: 305) and Cernohorsky (1972: 201).

*Description:* Shell (Fig. 24): Thick, mitriform, polished, 12–15 mm in length, with 9–10 adult whorls. Shell elongate-ovate to elongate-narrow, variable in color. Elongate-ovate forms with convex whorls, few to many prominent axial ribs, and often colored with brown flammules (Fig. 24A). Narrow-elongate forms often with numerous weak axial ribs (Fig. 24B), sides of whorls convex to straight and banded or plain. In all forms, body whorl 50% of shell length. Adult whorls finely perforate (Fig. 24A). Protoconch and upper adult whorls often eroded and pitted (Fig. 24E, H). Aperture elongate-ovate, with thick outer lip. One large col-

umellar fold on upper half of upper columella, dorsal to two smaller folds (Fig. 24A, C), all folds perpendicular to the columella axis. Smaller folds smooth, larger fold with 3–4 ridges constructed of a series of overlapping or imbricate plates (Fig. 24D). Plates unidirectional, oriented opposite to coiling direction. Six to seven unequal palatal teeth deep inside outer lip, with largest denticle in middle of row. Rudimentary palatals usually present just inside outer lip. Protoconch smooth, heterostrophic, oriented 120° to teleoconch, 40–45% submerged in first adult whorl, with earliest portion of protoconch partially submerged (Fig. 24E, H). Operculum tan, elongate-ovate, notched to accommodate largest columellar fold (Fig. 24I).

Head-foot (Fig. 20C): White, with aggregates of large numerous white cells between and posterior to eyes, on tentacles, mentum, and foot, particularly concentrated just anterior of operculum. Anterior end of foot wide anteriorly, with slight medial indentation and acute antero-lateral projections. Foot narrowing posterior to propodium, widening, then tapering again to blunt apex. Tentacles triangular, connate, medially notched, laterally folded; tentacular pads absent. Eyes black, subepithelial, spherical, on median side of tentacles. Mentum retuse, with medial longitudinal groove (Fig. 11D). Columellar and retractor muscles as in *P. sulcata*. Visceral mass containing reddish-dark brown digestive tissue cells, translucent to opaque reproductive structures. Visceral coils partially covered by densely packed white cells.

Alimentary tract (Fig. 21A): Introvert-proboscis arrangement and aperture, buccal sac, buccal pump and remainder of alimentary tract as in *P. sulcata*. Retractor muscle arrangement as in *P. sulcata*.

Pallial cavity (Fig. 1B): Mantle and mantle organs typical for the Pyramidellinae. Mantle edge coarsely crenulate. Ventral and dorsal ciliated strips joining on mantle roof at posterior end of mantle cavity. Very large, pigmented mantle organ containing variably sized opaque to clear cells with a few peripheral yellow and red cells, narrowing posteriorly, terminating at convergence of dorsal and ventral ciliated strips. Organ releasing a small amount of opaque substance flecked with white. Large, yellow gland beneath ventral ciliated strip, extending length of strip, containing primarily large yellow cells and a small number of cells filled with red or white contents. Bright yellow exudate secreted

when snail disturbed (Table 5). Osphradium as in *P. sulcata*. Thin line of white glandular cells extending anteriorly from juncture of ciliated strips atop gill, terminating at anterior edge of mantle roof. Gill as in *P. sulcata*.

Reproductive system: Typical of pyramidellids in this study (Fig. 5A). Penial complex like that of *P. sulcata* (Fig. 22A).

Nervous system: Typical of the Pyramidellinae (Figs. 6A&B).

*Ecology and Distribution:* *Pyramidella mitralis* occurs intertidally to subtidally on sand flats throughout the Indo-Pacific (Cernohorsky, 1972). This snail remains buried during the day and is epifaunal at night (this study). Studies in Mozambique showed that this species occurs with the enteropneust *Ptychodera flava*, which may serve as its host (MacNae & Kalt, 1958).

Subfamily Turbonillinae Simroth, 1907  
Genus *Turbonilla* Risso, 1826

*Turbonilla* Risso, 1826: 224. Type species: *Turbonilla typica* Dall & Bartsch, 1903 (new name for *Turbonilla plicatula* Risso, 1826, non *Turbo plicatula* Brocchi, 1814), by subsequent designation of Dall & Bartsch, in Arnold, 1903:269. See Remarks below.

*Diagnosis:* Shell white and lanceolate, 9 mm in length, with 10–12 adult whorls. Whorls slightly convex to straight. Each whorl with prominent axial ribs, extending whorl length, except on body whorl, where axial ribs terminate prior to base. Intervening spaces present between ribs. Body whorl 20% of shell length. Umbilicus absent. Protoconch smooth, sinistrally heterostrophic, perpendicular to teleoconch, partially submerged in first adult whorl. Aperture squarish, with straight outer lip and slightly flared base. Columellar folds absent. Operculum tan, lenticular, with subcentric nucleus. Head-foot white. Short foot, anteriorly truncated, with lateral projections, tapered posterior. Tentacles elongate, subtriangular, connate, ventrolaterally folded; tentacular pads absent. Eyes black, subepithelial on median side of tentacles. Mentum incised, with shallow, longitudinal groove. Introvert opening medial on anterior mentum tip. Buccal sac composed of sucker, sheathed stylet, mouth/stylet aperture and stylet bulb. Penis extending through nerve ring beside proboscis. Anterior portion

of penis with several lateral rows of minute cuticular hooks.

*Remarks:* Risso (1826) introduced *Turbonilla* without designating a type species. He included four species in the new genus: *Turbonilla costulata* Risso, 1826; *Turbo gracilis* Brocchi, 1814; and *Turbo plicatula* Risso, 1826; and *Turbonilla humboldti* Risso, 1826. Almost all authors show the type species of *Turbonilla* either as *Turbo lacteus* Linnaeus, 1758, or as *Turbo elegantissimus* Montagu, 1803, often with the later in the synonymy of former. However, neither are originally included species, and are therefore, not eligible for type designation. Powell (1979: 256) shows the type species as *T. striata* Montagu, by subsequent designation of Gray (1847). This is not correct because Gray (1847: 160) listed *T. elegantissima* as the type species. A search of the literature has revealed no source for "*T. striata* Montagu," and this name is evidently a *lapsus calami*.

The earliest apparent valid type designation is that of Dall & Bartsch (in Arnold, 1903), in which they propose the new name *Turbonilla typica* as a replacement name for *T. plicatula* Risso, 1826, not *Turbo* (= *Turbonilla*) *plicatula* Brocchi. Although there is no internal evidence, other than the specific name, that Risso was simply transferring Brocchi's species to his new genus, many authors have considered this to be the case, with Bronn (1843: 1328) apparently the first to do so. Arnaud (1978: 129), for Risso's *T. plicatula*, stated: "C'est *Turbo plicatulus* Brocchi, 1814, annexé par Risso!"

#### *Turbonilla hemphilli* Bush, 1899

*Turbonilla hemphilli* Bush, 1899: 169, pl. 8, fig. 3. (Holotype: ANSP 79013; type locality: Sarasota Bay, Florida); Andrews, 1971: 132; Abbott, 1974: 302–303, fig. 3682.

*Turbonilla unilirata* Bush, 1899: 165, pl. 8, fig. 6. (Holotype: ANSP 79010; type locality: St. Thomas, West Indies).

*Turbonilla penistoni* Bush, 1899: 165–166, pl. 8, fig. 14. (Holotype: ANSP 70024; type locality: Bermuda).

*Turbonilla heilprini* Bush, 1899: 167–168, pl. 8, fig. 13. (Holotype: ANSP 79009; type locality: Bermuda).

*Turbonilla abrupta* Bush, 1899: 168, pl. 8, fig. 4. (Holotype: ANSP 79012; type locality: St. Thomas, West Indies).

*Synonymic Remarks:* Holotypes of the above species were examined and on the basis of shell morphology determined to be conspecific with *T. hemphilli*. Because these names were all proposed in the same work, *T. hemphilli* is here selected as senior synonym under the Principle of the First Reviser (I.C.Z.N. Article 24).

*Description:* Shell (Fig. 25): Thick, dull white, acutely lanceolate, 7–8 mm in length, composed of 12–13 adult whorls with sides straight to slightly convex (Fig. 25A). Whorls with 17–18 axial ribs. Except for body whorl, axial ribs the length of each whorl, with an elongate rectangular depression between each rib (Fig. 25B). Axial ribs on body whorl terminating at one-half of whorl's length. Body whorl 20% of shell length. Adult whorls etched by numerous fine prosocline growth lines. Aperture subquadrate, with base of outer lip slightly flared. Columellar folds absent. Protoconch smooth, sinistrally heterostrophic, oriented 90° to teleoconch axis, submerged 5–10% in first adult whorl, with earliest portion of protoconch exposed (Fig. 25C–E). Operculum brown, lenticular, with subcentric nucleus (Fig. 25F, G).

Head-foot (Fig. 26A): Opaque, with a large number of white cells scattered throughout. Propodium wide, with shallow medial indentation. Posteriorly the foot narrowing sharply to a blunt tip. Attachment thread absent. Tentacles elongate, subtriangular, connate, ventro-laterally folded; tentacular pads absent. Eyes black, subepithelial, round to kidney-shaped, on median side of tentacles. Mentum incised, with rounded antero-lateral edges and shallow longitudinal groove (Fig. 11E). Highly coiled visceral mass of grey and green digestive cells and opaque reproductive organs.

Alimentary tract (Fig. 21B): When retracted, introvert-proboscis extending posteriorly from its aperture located antero-medially on mentum tip to enter cephalic hemocoel. Introvert joining buccal sac, which joins a very short buccal pump divided into anterior (bp1) and posterior sections (bp2); bp2 four times length of bp1. Anterior esophagus originating on ventral surface of alimentary tract at bp1-bp2 juncture, joining posterior esophagus and paired salivary glands to form a four-way junction. Posterior esophagus extending into visceral mass and joining stomach. Salivary gland ducts extending anteriorly within walls of anterior esophagus. At convergence of an-

terior esophagus and buccal pump, ducts exiting and entering stylet bulb. Salivary glands attached distally to alimentary tract at anterior portion of posterior esophagus.

Pallial cavity (Fig. 1C): Mantle and mantle organs characteristic of subfamily Turbonillinae. Mantle edge etched by fine lines. Mantle floor and roof darkly pigmented. Ventral and dorsal ciliated strips joining posteriorly on mantle roof of mantle cavity. Large, rectangular, oblong pigmented mantle organ composed primarily of clear cells surrounding a narrow oblong region of bright yellow cells. Gland beneath ventral ciliated strip extending posteriorly from mantle edge to convergence of ciliated strips. Anterior quarter of this gland composed of large cells containing a thick yellow exudate, whereas remainder composed of cells filled with a white substance. Both ventral ciliated strip gland and pigmented mantle organ secreting a viscous yellow exudate when snail disturbed (Table 5). Gill absent.

Reproductive system: Typical of pyramidellids herein (Fig. 5B). Penis sharing nerve ring with proboscis (Fig. 22B). Penis anterior, attenuate, with a deep medial groove and several lateral rows of minute cuticular hooks (Fig. 27A), widening posteriorly, becoming elongate and bulbous. Sperm sac perpendicular to long axis of penis.

Nervous system: Typical of known pyramidellids (Fig. 6A).

*Ecology and Distribution:* *Turbonilla hemphilli* occurs subtidally to intertidally in grass/mud flats from Bermuda to Texas and south to St. Thomas, West Indies (Abbott, 1974). Host unknown.

### Genus *Houbricka* new genus

Type species: *Turbonilla incisa* Bush, 1899, here designated.

*Diagnosis:* Lanceolate, white to orange, with brown band encircling lower portion of each whorl, 6 mm in length, composed of 7–8 slightly convex whorls. Each whorl with numerous strong axial ribs separated by 6–7 incised spiral shallow grooves between and perpendicular to intercostal spaces; sculpturing replaced on lower one-third of body whorl by fine spiral lines. Body whorl 30% of shell length. Protoconch smooth, sinistrally heterostrophic, oriented 90° to teleoconch, submerged 5–10% in adult whorl. Aperture elon-

gate-ovate, with base of outer lip weakly flared. Columellar folds absent. Operculum brown, lenticular, with subcentric nucleus. Head-foot white to reddish pink, with large white cells dispersed throughout. Anteriorly, foot flared slightly, not bifurcate. Foot narrowing posterior to propodium, then widening and ending in blunt apex. Attachment thread absent. Tentacles elongate, subtriangular, connate, ventro-laterally folded; tentacular pads absent. Eyes black, subepithelial, ovate, on median side of tentacles. Mentum incised, with rounded lateral edges and shallow longitudinal groove. Introvert extending posteriorly from its medial aperture at anterior mentum tip to enter cephalic hemocoel. Introvert forming an S-shaped loop and continuing posteriorly to join buccal sac, which is composed of sucker, sheathed stylet, mouth/stylet aperture, and stylet bulb. Buccal sac joining a buccal pump, which is divided into anterior (bp1) and posterior sections (bp2); laterally flattened bp2 seven times length of bp1. Anterior esophagus originating at juncture of bp1-bp2, extending posteriorly to join posterior esophagus and paired salivary glands, forming a four-way junction. Salivary gland ducts highly folded, attached to exterior of anterior esophagus. Ducts extend from anterior esophagus to just posterior of buccal pump-buccal sac juncture, where they detach and enter stylet bulb. Tuberculate, inflated posterior esophagus extending posteriorly to enter visceral mass to join stomach. Salivary glands attached distally to alimentary tract at anterior portion of posterior esophagus. Retracted, folded scoop-shape penis within cavity that opens medial and ventral to mentum outside nerve ring.

*Remarks:* The new genus introduced here has been named to honor the late Dr. Richard S. Houbrick for his very significant contributions to the science of malacology.

The justification for naming a new genus is based on anatomical differences between *Houbricka incisa* and our current understanding of the genus *Turbonilla*. Regardless of the nomenclatural problems outlined above, the anatomies of certain species within the genus *Turbonilla* are well known (e.g., *Turbonilla elegantissima*, *T. jeffreysii*). When *T. hemphilli* is compared to these taxa, this species, and not *H. incisa*, are very similar. Moreover, the only taxa that are conchologically similar to *Houbricka incisa*, are subgenera (*sensu* Dall & Bartsch, 1909), and their anatomy is un-

known. Therefore, until the type species of these subgenera are examined in greater detail, these names should not be used.

*Houbricka incisa* (Bush, 1899)

*Turbonilla incisa* Bush, 1899: 156–157, pl. 8, fig. 12. (Holotype: ANSP 62800; type locality: West Florida); Abbott, 1974: 306, fig. 3781.

**Remarks:** The holotype is a poor specimen, which is badly worn, with both aperture and protoconch broken.

**Description:** Shell (Fig. 28): Lanceolate, white to orange, with brown band encircling lower portion of each whorl, 6 mm in length, composed of 7–8 slightly convex whorls (Fig. 28A). Each whorl with numerous strong axial ribs separated by 6–7 incised spiral shallow grooves between and perpendicular to intercostal spaces (Fig. 28B), this sculpture replaced on lower one-third of body whorl by fine spiral lines. Body whorl 30% of shell length. Aperture elongate-ovate, with base of outer lip weakly flared. Columellar folds absent. In a few specimens, slight swellings present on columella deep inside the body whorl. Protoconch smooth, sinistrally heterostrophic, oriented 90° to teleoconch, submerged 5–10% in first adult whorl, with earliest portion of protoconch exposed (Fig. 28C, E). Operculum brown, lenticular, with subcentric nucleus (Fig. 28F, G).

**Head-foot** (Fig. 26B): White to reddish pink (presence of hemoglobin?), with large white cells dispersed throughout. Anteriorly, foot flared slightly, not bifurcate. Foot narrowing posterior to propodium, then widening and ending in blunt apex. Attachment thread absent. Tentacles elongate, subtriangular, connate, ventrolaterally folded; tentacular pads absent. Eyes black, subepithelial, ovate, on median side of tentacles. Mentum incised, with rounded lateral edges and shallow longitudinal groove (Fig. 11F). Visceral mass of grey, brown, orange or red digestive tissue cells and opaque to translucent reproductive organs.

**Alimentary tract** (Fig. 21C): Retracted introvert-proboscis extending posteriorly from its medial aperture at anterior mentum tip to enter cephalic hemocoel. Introvert forming S-shaped loop, continuing posteriorly to join buccal sac. Buccal sac joining buccal pump,

which is divided into anterior (bp1) and posterior sections (bp2); laterally flattened bp2 seven times length of bp1. Anterior esophagus originating at bp1-bp2 juncture, extending posteriorly to join posterior esophagus and paired salivary glands, forming a four-way junction. Salivary gland ducts highly folded and attached to exterior of anterior esophagus. Ducts extending from anterior esophagus to just posterior of buccal pump-buccal sac juncture, where they detach and enter stylet bulb. Tuberculate, inflated posterior esophagus extending posteriorly to enter visceral mass and join the stomach. Salivary glands attached distally to alimentary tract at anterior portion of posterior esophagus.

**Pallial cavity** (Fig. 1A, C): Mantle and mantle organs only generally like those of the subfamily Turbonillinae. Mantle edge crenulate. Dorsal surface of mantle roof with scattered flecks of black pigment. A line of subepithelial black cells extending posteriorly across the left side of mantle. Ventral and dorsal strips converge posteriorly on roof of mantle cavity. Small, oblong pigmented mantle organ (similar to the pigmented mantle organ present in the Odostominae) containing clear cells, cells filled with yellow exudate, and a few scattered cells containing a red substance, this organ secreting a thick, bright yellow exudate when snail disturbed (Table 5). Gland beneath ventral ciliated strip, composed of large, black cells within a transparent matrix, extending the length of the strip. Gill absent.

**Reproductive system:** Typical of pyramidellids in this study (Fig. 5B). Penis outside and ventral to nerve ring (Fig. 22C). Retracted, folded penis within pocket that opens medial and ventral to mentum. Paired retractor muscles anchor penis to pocket floor. Tapered, dorsoventrally flattened anterior penis tip, scoop-shape with wide, medial groove (Fig. 27B).

**Nervous system:** Typical of known pyramidellids (Fig. 6A).

**Ecology and Distribution:** *Houbricka incisa* occurs intertidally to subtidally on both the east and west coasts of southern Florida to Texas (Abbott, 1972; this study). Host unknown.

Genus *Tathrella* Laseron, 1959

*Tathrella* Laseron, 1959: 218. Type-species: *Tathrella iredalei* Laseron, 1959, by original designation.

*Diagnosis:* Shell white, transparent elongate, conical, 6 mm in length, with 7–8 adult whorls. Convex whorls with numerous small axial ribs. Body whorl 40% of shell length. Umbilicus absent. Protoconch smooth, sinistrally heterostrophic, oriented 95° to teleoconch, partially submerged in first adult whorl. Aperture ovate, with base of outer lip slightly flared. Columellar folds absent. Head-foot white with medial black stripe extending from anterior end of mentum onto mantle floor. Anterior portion of foot with medial indentation, flared lateral projections. Foot narrowing posteriorly to a blunt tip. Pedal gland producing an attachment thread. Tentacles cylindrical, slender, not connate; tentacular pads absent. Eyes subepithelial, on median side of tentacles. Mentum incised, with rounded, lateral projections and longitudinal groove. Introvert-proboscis aperture medial on anterior mentum apex. Introvert joining buccal sac, which is composed of sucker, sheathed stylet, mouth-stylet aperture, and stylet bulb. Buccal sac joining buccal pump, which is composed of two sections (bp1 and bp2). Anterior esophagus originating at bp1-bp2 juncture, extending posteriorly and joining posterior esophagus and paired salivary glands. Salivary gland ducts attached to exterior of anterior esophagus. Ducts extending from anterior esophagus-buccal pump juncture to enter stylet bulb. Penis with sperm sac, sharing nerve ring with proboscis.

*Remarks:* The monotypic genus, originally described from the shell of a single specimen was collected in 20 fms. (not 11 fms., as stated by Laseron, 1959) off Port Curtis, Queensland, Australia.

*Tathrella iredalei* Laseron, 1959

*Tathrella iredalei* Larson, 1959: 218, fig. 101. (Holotype: AMS 105285, type locality: Port Curtis, Gladstone, Queensland, Australia).

*Pyrgiscus* sp. Cumming, 1988.

*Turbonilla* sp. Cumming, 1993.

*Description:* Shell (Fig. 29): Thin, chalky white, translucent, 5–6 mm in length, composed of 7–9 convex whorls. Body whorl 40% of shell length (Fig. 29A). Adult whorls with a number of slender axial ribs and microscopic orthocline growth lines. Aperture elongate-ovate, with outer lip flared at base (Fig. 29B).

Columella thick, without columellar folds. In some specimens, 1–4 swellings present deep within body whorl on columella (Fig. 29C). Protoconch smooth, sinistrally heterostrophic, oriented 95° to teleoconch axis, submerged 10–15% in first adult whorl, with earliest portion of protoconch partially exposed (Fig. 29D, F). Operculum brown, lenticular, with subcentric nucleus (Figs. 29G, H).

Head-foot (Fig. 26C): White with prominent black stripe extending from anterior mentum tip across the head and, in some individuals, onto mantle floor. Propodium with moderate medial indentation and flared lateral projections. Foot narrowing posterior to propodium, then widening and terminating in blunt tip. Black lines of pigment of varying length and definition typically on dorso-lateral surface of foot. Opening to pedal gland a slit on postero-ventral surface of foot extending one fourth of foot's length anteriorly from posterior end. Pedal gland producing an attachment thread. Tentacles cylindrical, long, not connate; tentacular pads absent. Eyes black, subepithelial, on median side of tentacles. Mentum incised, long, with knob-like anterolateral projections (Fig. 11G). Short, corpulent visceral coil of light orange, gray, or creamy white digestive tissue cells and opaque reproductive organs.

Alimentary tract (Fig. 21D): When retracted, introvert/proboscis extending posteriorly from its medial aperture on anterior mentum tip to enter cephalic hemocoel and join buccal sac. Buccal sac connecting to a moderately short buccal pump. Buccal pump divided into anterior (bp1) and posterior sections (bp2); bp2 five times length of bp1. Short anterior esophagus joining buccal pump just posterior of buccal sac-buccal pump juncture. Anterior esophagus continuing posteriorly to join posterior esophagus and salivary glands to form a four-way junction. Long, highly coiled posterior esophagus extending to enter visceral mass and terminate at stomach. Salivary gland ducts attached to outer surface of anterior esophagus. At convergence of anterior esophagus and buccal pump, salivary ducts extend anteriorly to enter stylet bulb. Salivary glands attached distally to alimentary tract at anterior portion of posterior esophagus.

Pallial cavity (Figs. 1A, C): Mantle and mantle organs generally as described for the Turbonillinae. Mantle edge finely scalloped. Ventral and dorsal ciliated strips join posteriorly on mantle roof of mantle cavity; strips bi-

sected by a thin line of brown, glandular cells that extend the length of mantle cavity. Small, oblong pigmented mantle organ (similar to same organ in Odostominae) composed primarily of cells containing a yellow exudate and a few cells filled with white contents. Gland, beneath ventral ciliated strip extending 50–60% of strip's length. Gland filled with cells containing a bright yellow exudate. Snail exuding copious amounts of exudate from ventral ciliated strip gland and a lesser amount from pigmented mantle organ when disturbed (Table 5). Gill absent.

Reproductive system: Typical of pyramidellids examined this study (Fig. 5B). Penis sharing nerve ring with proboscis and when protracted, extending through a medial opening ventral to mentum (Fig. 22D). Posteriorly, penis continuing into cephalic hemo-coel, looping once, and attaching ventrally to columellar muscle. Anterior of penis medially grooved and ciliated. A slender duct leading distally to bulbous sperm sac present perpendicular to anterior portion of penis sheath.

Nervous system: Characteristic of known pyramidellids (Fig. 6A).

*Ecology and Distribution:* *Tathrella iredalei*, which parasitizes various *Tridacna* species, has inadvertently been sent to mariculture facilities throughout the Indo-Pacific (e.g., to Australia, Philippines, Guam, and the Solomon Islands) in shipments of *Tridacna*. As a result, this snail has been introduced into areas where it does not naturally occur, making its original geographic distribution difficult to determine.

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## LITERATURE CITED

- AARTSEN, J. J. VAN, 1977, European Pyramidellidae: I. *Chrysallida*. *Conchiglie*, 13: 49-64.
- AARTSEN, J. J. VAN, 1981, European Pyramidellidae: II. *Turbonilla*. *Bollettino Malacologico* 17: 61-88.
- AARTSEN, J. J. VAN, 1987, European Pyramidellidae: III. *Odostomia* and *Ondina*. *Bollettino Malacologico*, 23: 1-34.
- ABBOTT, R. T., 1974, *American seashells*, 2nd ed. Van Nostrand Reinhold Company, New York, 663 pp., 24 pls.
- ADAMS, A., 1854, Monographs of the genera *Eulima*, *Niso*, *Leiostraca*, *Obeliscus*, *Pyramidella*, and *Monoptygma*. In: G. B. SOWERBY, *Thesaurus Conchyliorum*. London, 2: 793-825, pls. 169-172.
- ADAMS, A., 1854-5, A monograph of *Pyramidella*, a genus of gasteropodous Mollusca, belonging to the family Pyramidellidae. *Proceedings of the Zoological Society of London*, for 1853: 176-178, pl. 20. (p. 176, Dec. 1854; pp. 177-178, May 1855)
- ADAMS, A., 1861, On a new genus and some new species from the North of China. *Annals and Magazine Natural History*, 7: 295-299.
- ADAMS, C. B., 1839, Observations on some species of the marine shells of Massachusetts, with descriptions of five new species. *Boston Journal of Natural History*, 2: 262-288, pl. 4.
- ADAMS, C. B., 1845, Specierum novarum conchyliorum, in Jamaica repertorum, synopsis. *Proceedings of the Boston Society of Natural History*, 2: 1-17.
- ADAMS, C. B., 1852, *Catalogue of shells collected at Panama with notes on their synonymy, station, and geographical distribution*. R. Craighead, Printer, New York, viii + 334 pp.
- AMIO, M., 1963, A comparative embryology of marine gastropods, with ecological considerations. *Shimonoskei University Fisheries Journal*, 12: 15-144.
- ANDREWS, J., 1971, *Sea shells of the Texas coast*. University of Texas Press, Austin and London, xvii + 298 pp.
- ANDREWS, J., 1977, *Shells and shores of Texas*. University of Texas Press, Austin and London 365.
- ANKEL, W. E., 1949a, *Die Nahrungsaufnahme der Pyramidelliden*. *Verhandlungen Deutsche Zoologische Gesellschaft (Kiel)*, 1948: 478-484.
- ANKEL, W. E., 1949b, Die Mundbewaffnung der Pyramidelliden. *Archiv für Molluskenkunde*, 77: 79-82.
- ANKEL, W. E., 1959, Beobachtungen an Pyramidelliden des Gullmar-Fjordes. *Zoologischer Anzeiger*, 162: 1-21.
- ANKEL, W. E. & A. M. CHRISTENSEN, 1963, Non-specificity in host selection by *Odostomia scalaris* Macgillivray. *Videnskabelig Meddelelse fra Dansk Naturhistorisk Forening*, 125: 321-325.
- ARNAUD, P. M., 1978, Révision des taxa malacologiques Méditerranéens introduits par Antoine Risso. *Annales du Muséum d'Histoire Naturelle de Nice*, 5: 101-150.
- BAKER, F., G. D. HANNA & A. M. STRONG, 1928, Some Pyramidellidae from the Gulf of California. *Proceedings of the California Academy of Sciences*, (4)17: 205-246, pls. 11-12.
- BARTSCH, P., 1909, Pyramidellidae of New England and the adjacent region. *Proceedings of the Boston Society of Natural History*, 34: 67-113, pls. 11-14.
- BARTSCH, P., 1917, Descriptions of new west American marine mollusks and notes on previously described forms. *Proceedings of the United States National Museum*, 52: 637-681, pls. 42-47.
- BARTSCH, P., 1955, The pyramidellid mollusks of the Pliocene deposits of North St. Petersburg, Florida. *Smithsonian Miscellaneous Collections*, 125: i-iii, 1-102, pls. 1-18.
- BERNARDI, A. C., 1859, Descriptions d'espèces nouvelles. *Journal de Conchyliologie*, 7:386, pl. 13, figs 1,4.
- BIELER, R., 1992, Gastropod phylogeny and systematics. *Annual Review of Ecology and Systematics*, 23: 311-38.
- BOETTGER, C. R., 1955, Die Systematik der euthyneuren Schnecken. *Zoologischer Anzeiger, Supplement*, 18: 253-280.
- BOSS, K. J., 1982, Classification of Mollusca. In: *Synopsis and classification of living organisms*, S. P. PARKER, ed. McGraw-Hill Book Company, New York, Volume 1: 945-1166; Volume 2: 1092-1096.
- BOSS, K. J. & A. S. MERRILL, 1965, Degree of host specificity in two species of *Odostomia* (Pyramidellidae: Gastropoda). *Proceedings of the Malacological Society of London*, 36: 349-355, pl. 15.
- BRANDT, R. H. M., 1968, Descriptions of new non-marine mollusks from Asia. *Archiv für Molluskenkunde*, 98: 213-289, pls. 8-10.
- BROCCHI, G., 1814, *Conchiologia fossile subapennina, con osservazioni geologiche sugli Apennini e sul suolo adiacente*. Stamperia Reale, Milano. 2 vols. [1: 1-240, 2: 241-712, pls. 1-16. Milano.
- BROWN, T., 1927, *Illustrations of the conchology of Great Britain and Ireland*. London, i-v pp., pls. 1-52.
- BRONN, H. G., 1848, *Index palaeontologicus oder übersicht der bis jetzt bekannten fossilen Organismen, unter mitwirkung der HH. Prof. H.R. Göppert und Herm. v. Meyer*. A. Nomenclator palaeontologicus, in alphabetischer Ordnung. E. Schweizerbart'sche, Stuttgart. lxxxiv + 1381 pp.
- BRUSCA, R. & G. BRUSCA, 1990, Phylum Mollusca. In: *Invertebrates*, ed. CAROL J. WIGG. Sinauer Associates, Inc., Sunderland, 922 pp.
- BULLOCK, R. & K. BOSS, 1971, Non-specificity of host-selection in the ectoparasitic snail *Odostomia (Menestho) bisuturalis* (Say) (Gastropoda: Pyramidellidae). *Breviora*, 363: 1-7.



- BUSH, K. J., 1899, Descriptions of new species of *Turbonilla* of the western Atlantic fauna, with notes on those previously known. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 52: 145–177, pl. 8.
- BUSH, K. J., 1909, Notes on the family Pyramidellidae. *American Journal of Science*, 27: 475–484.
- CARPENTER, J. M., 1988, Choosing among multistate equally parsimonious cladograms. *Cladistics*, 4: 291–296.
- CARPENTER, P. P., 1857, *Catalogue of the collection of Mazatlan shells in the British Museum: Collected by Fredrick Reigen*. Oberlin Press, Warrington, xii + 552 pp.
- CARPENTER, P. P., 1864, Supplementary report of the present state of our knowledge with regard to the mollusca of the west coast of North America. *Report of the British Association for the Advancement of Science*, for 1863: 517–686.
- CERNOHORSKY, W. O., 1972, *Marine shells of the Pacific*, Volume II. Pacific Publications, Sydney, 411 pp.
- CONRAD, T. A., 1843, Descriptions of a new genus and of twenty-nine new Miocene, and one Eocene, fossil shells of the United States. *Proceeding of the Academy of Natural Sciences of Philadelphia*, 1: 305–311.
- CUMMING, R., 1988, Pyramidellid parasites in giant clam mariculture systems. Pp. 231–236, in: *Giant clams in Asia and the Pacific*. J. W. COPLAND & J. S. LUCAS, eds. Australian Centre for International Agricultural Research, Canberra 1988.
- CUMMING, R., 1993, Reproduction and variable larval development of an ectoparasitic snail, *Turbonilla* sp. Pyramidellidae, Opisthobranchia, on cultured giant clams. *Bulletin of Marine Science*, 52: 760–771.
- DALL, W. H., 1884, On a collection of shells sent from Florida by Mr. Henry Hemphill. *Proceedings of the United States National Museum*, 6: 318–342, pl. 10.
- DALL, W. H., 1885, Notes on some Floridian land and fresh-water shells with a revision of the Auriculacea of the eastern United States. *Proceedings of United States National Museum*, 8: 255–289, pls. 17–18.
- DALL, W. H. & P. BARTSCH, 1903, Family LXIV. Pyramidellidae, pp. 269–285, pls. 1–4 (in part) In: R. ARNOLD, The paleontology and stratigraphy of the marine Pliocene and Pleistocene of San Pedro, California. *Memoirs of the California Academy of Sciences*, 3: 1–420, pls. 1–37.
- DALL, W. H. & P. BARTSCH, 1904, Synopsis of the genera, subgenera and sections of the family Pyramidellidae. *Proceedings of the Biological Society of Washington*, 17: 1–16.
- DALL, W. H. & P. BARTSCH, 1906, Notes on Japanese, Indopacific, and American Pyramidellidae. *Proceedings of the United States National Museum*, 30: 321–369, pls. 17–26.
- DALL, W. H. & P. BARTSCH, 1909, A monograph of west American pyramidellid mollusks. *Bulletin of the United States National Museum*, 68: 1–258, pls. 1–30.
- DAVIS, G. M., 1979, The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae. *Academy of Natural Sciences of Philadelphia, Monograph* 20: 1–120.
- DEJONG, K. M. & H. E. COOMANS, 1988, *Marine gastropods from Curaçao, Aruba, and Bonaire*. E.J. Brill Publishing Company, Lieden, Netherlands, 153 pp., pls. 1–47.
- DILLWYN, L. W., 1817, *A descriptive catalogue of Recent shells, arranged according to the Linnaean method; with particular attention to synonymy*. Printed for John & Arthur Arch, Cornhill, London, Volume 2: 581–1092.
- D'ORBIGNY, A., 1839, *Mollusques, échinodermes, foraminifères et polypiers, recueillis aux Iles Canaries par MM. Webb and Berthelot*. Histoire Naturelle des Iles, Zoologie, 2: 1–117.
- FABER, M. J., 1988, Studies on West Indian marine mollusks 13. The malacological taxa of Gordon W. Nowell-Usticke. *De Kreukel*, 24: 67–102.
- FARRIS, J. S., 1982, The information content of the phylogenetic system. *Systematic Zoology*, 28: 386–401.
- FARRIS, J. S., 1983, *The logical basis of phylogenetic analysis*. In: *Advances in Cladistics*. N. PLATNICK & V. FUNK, eds. Columbia University Press, New York, Vol. 2: 7–36.
- FARRIS, J. S., 1988, *A PC-DOS program for phylogenetic systematics*. Port Jefferson Station, New York.
- FARRIS, J. S., 1989, The retention index and the rescaled consistency index. *Cladistics*, 7: 1–28.
- FISCHER, P.-H., 1880–1887, *Manuel de conchyliologie et de paléontologie conchyliologique, ou histoire naturelle des mollusques vivants et fossiles*. Savy: Paris, xxiv., 1369 pp., pls. 1–23. (Pyramidellidae: pp. 784–790; January 1885).
- FLEMING, J., 1813, Conchology. In: *Brewster's Edinburgh encyclopaedia*. William Brown Printer, Philadelphia, volume 7: 55–107.
- FOLIN, L. DE, 1885, Constitution méthodique rationnelle et naturelle de la famille des Chemnitzidae *Annales Société d'Agriculture de Lyon*, (7)3: 1–16.
- FRETTER, V., 1951, *Turbonilla elegantissima* (Montagu) a parasitic opisthobranch. *Journal of the Marine Biological Association of the United Kingdom*, 30: 37–47.
- FRETTER, V. & A. GRAHAM, 1949, The structure and mode of life of the Pyramidellidae, parasitic opisthobranchs. *Journal of Marine Biological Association of the United Kingdom*, 28: 493–532.
- FRETTER, V. & A. GRAHAM, 1962, *British prosobranch molluscs*. Ray Society, London, 755 pp.
- FRETTER, V., A. GRAHAM & E. ANDREWS, 1986, The prosobranch molluscs of Britain and Denmark. Part 9-Pyramidellacea. *Journal of Molluscan Studies, Suppl.* 16: 557–649.

- GHILSEN, M., 1966, Reproductive function and the phylogeny of opisthobranch gastropods. *Malacologia*, 3: 327–78.
- GOFAS, S., J. P. ALFONSO & M. BRANDAO, 1981, *Conchas e moluscos de Angola*. Universidade Agostinho Neto/Elf Aquitaine Angola, 139 pp.
- GOLIKOV, A. N. & Y. I. STARBOGATOV, 1975, Systematics of prosobranch gastropods. *Malacologia*, 15: 185–232.
- GOSLINER, T. M., 1981, Origins and relationships of primitive members of the Opisthobranchia (Mollusca, Gastropoda). *Biological Journal of the Linnean Society*, 16: 197–226.
- GOULD, A. A., 1841, *Report on the invertebrata of Massachusetts, comprising the Mollusca, Crustacea, Annelida, and Radiata*. Zoological and Botanical Survey of the State. Folsom, Wells, & Thurston, Cambridge, xiii + 373 pp., 15 pls.
- GRAHAM, A., 1988, *Molluscs: prosobranch and pyramidellid gastropods. Keys and notes for the identification of the species*. No. 2, 2nd ed. Pub. for the Linnean Society of London and The Estuarine and Brackish-Water Sciences Association by E. J. Brill & Dr. W. Backhuys. Leiden, New York, Kobenhavn, Köln, 655 pp.
- GRAY, J. E., 1840, [Mollusca], pp. 86–89, 106–156. In: *Synopsis of the contents of the British Museum*. 42nd edition, G. Woodfall and Son, London. 370 pp. (see Sherborn, 1934, for dates and pagination of various editions).
- GRAY, J. E., 1847, A list of the genera of Recent Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London*, for 1847: 129–219.
- HADFIELD, M. & M. SWITZER-DUNLAP, 1984, Opisthobranchs. In: *The Mollusca; reproduction*. A. S. TOMPA, N. H. VERDONK & J. A. VAN DEN BIGGELAAR, eds. Academic Press, Inc. New York, Vol. 7: 209–350.
- HARRY, H., 1984, The animals of some shelled opisthobranch snails of Galveston. *Texas Conchology*, 20: 68–75.
- HASZPRUNAR, G., 1985a, The fine morphology of the osphradial sense organs of the Mollusca. II. Allogastropoda (Architectonicidae, Pyramidellidae). *Philosophical Transactions of the Royal Society, London*, (B)307: 497–505.
- HASZPRUNAR, G., 1985b, The Heterobranchia—a new concept of the phylogeny of the higher Gastropoda. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, 23: 15–37.
- HASZPRUNAR, G., 1985c, On the innervation of gastropod shell muscles. *Journal of Molluscan Studies*, 51: 309–314.
- HASZPRUNAR, G., 1988a, On the origin and evolution of major gastropod groups, with special reference to the Streptoneura. *Journal of Molluscan Studies*, 54: 367–441.
- HASZPRUNAR, G., 1988b, A preliminary phylogenetic analysis of the streptoneurous Gastropoda. In: Prosobranch Phylogeny. W. F. PONDER, ed. *Malacological Review*, Suppl. 4: 64–84.
- HASZPRUNAR, G., 1990, Towards a phylogenetic system of Gastropoda Part 1: Traditional methodology—a reply. *Malacologia*, 32: 195–202.
- HEALY, J. M., 1988a, Sperm morphology and its systematic importance in the Gastropoda. In: Prosobranch phylogeny, W. F. PONDER, ed. *Malacological Review*, Suppl. 4: 251–266.
- HEALY, J. M., 1988b, The ultrastructure of spermatozoa and spermiogenesis in pyramidellid gastropods, and its systematic importance. *Helgolander Meeresuntersuchungen* 42: 303–318.
- HEALY, J. M., 1993, Comparative sperm ultrastructure and spermiogenesis in basal heterobranch gastropods (Valvatoidea, Architectonicoidea, Rissoelloidea, Omalogyroidea, Pyramidelloidea) (Mollusca). *Zoologica Scripta*, 22: 263–276.
- HENDERSON, J. B. & P. BARTSCH, 1914, Littoral marine mollusks of Chincoteague Island, Virginia. *Proceedings of the United States National Museum*, 47: 411–421, pls. 13–14.
- HENNIG, W., 1966, *Phylogenetic systematics*. University of Illinois, Urbana, 263 pp.
- HOLMES, F. S., 1858–1860, *Post-Pleiocene fossils of South Carolina*. Russell & Jones, Charleston, South Carolina, 122 pp., pls. 1–28.
- HÖISAETER, T., 1965, Spermatophores in *Chrysalida obtusa* (Brown) (Opisthobranchia, Pyramidellidae). *Sarsia*, 18:63–68.
- HOLTEN, H. S., 1802, *Enumeratio systematica conchyliorum beat. J. H. Chemnitzii*. Copenhagen, 88 pp.
- HUBER, G., 1987, *Zum cerebralen Nervensystem mariner Heterobranchia (Gastropoda)*. Dissertation am Institut für Zoologie der Universität Wien, Wien Austria.
- HUBER, G., 1993, On the cerebral nervous system of marine Heterobranchia (Gastropoda). *Journal of Molluscan Studies*, 59: 381–420.
- HUMPHREY, G., 1797, *Museum Calonianum*. London, vii + 84 pp. (Rejected for nomenclatural purposes in I.C.Z.N. Opinion 51).
- HYMAN, L., 1967, *The Invertebrates: Mollusca I (volume I)*. Aplacophora, Polyplacophora, Monoplacophora, Gastropoda. *The coelomate Bilateria*. McGraw-Hill Book Company, New York, 792 pp.
- JONES, T. R., A. K. KLUGE & A. J. WOLF, 1993, When theories and methodologies clash: a phylogenetic reanalysis of the North American ambystomatid salamanders (Caudata: Ambystomatidae). *Systematic Biology*, 42: 92–102.
- KAY, E. A., 1979, Hawaiian Marine Shells. Reef and shore fauna of Hawaii. Section 4: Mollusca. *Bishop Museum Special Publication*, 64(4): xvii + 653 pp.
- KLUGE, A. & J. S. FARRIS, 1969, Quantitative phylogenetics and the evolution of anurans. *Systematic Zoology*, 18: 1–32.
- KNIGHT, J. B., L. R. COX, A. M. KEEN, A. G. SMITH, R. L. BATTEN, E. L. YOCHENSEN, N. H. LUDBROOK, R. ROBERTSON, C. M. YONGE, & R. C. MOORE, 1960, *Mollusca I*. In: *Treatise on*

- Invertebrate Paleontology. R. C. MOORE & C. W. PI-TRAT, eds. Geological Society of America and University of Kansas Press. 351 pp.
- KOOL, S. P., 1993, Phylogenetic analysis of the Rapaninae (Neogastropoda:Muricidae). *Malacologia*, 35: 155-259.
- KRISTENSEN, J. H., 1970, Fauna associated with the sipunculid *Phascolion strombi* (Montagu), especially the parasitic gastropod *Menestho diaphana* (Jeffreys). *Ophelia*, 7: 257-276.
- LAFOLLETTE, P., 1977, Inbreeding and intraspecific variation in *Chrysallida* Carpenter, 1857 (Gastropoda: Pyramidellidae). *The Western Society of Malacologists, Annual Report*, 10: 18-23.
- LAFOLLETTE, P., 1979, Observations on the larval development and behavior of *Chrysallida cincta* Carpenter, 1864 (Gastropoda: Pyramidellidae). *The Western Society of Malacologists, Annual Report*, 11: 31-34.
- LAMARCK, J. B. P. A., 1799, Prodrome d'une nouvelle classification des coquilles, comprenant une rédaction appropriée des caractères génériques, et l'établissement d'un grand nombre de genres nouveaux. *Mémoires de la Société d'Histoire Naturelle de Paris*, 1: 63-91.
- LASERON, C. F., 1959, The family Pyramidellidae (Mollusca) from Northern Australia. *Australian Journal of Marine and Freshwater Research*, 10: 177-267, figs. 1-213.
- LAWS, C. R., 1937a, Review of the Tertiary and Recent Neozelanic Pyramidellid Molluscs. No. 1. The genus *Turbonilla*. *Transactions of the Royal Society of New Zealand*, 66: 402-422, pls. 32-33.
- LAWS, C. R., 1937b, Ibidem. No. 2. The genus *Chemnitzia* lb., 67: 47-70.
- LAWS, C. R., 1937c, Ibidem. No. 3. Further turbonillid genera. lb., 67: 166-184.
- LAWS, C. R., 1937d, Ibidem. No. 4. The syrnelid genera. lb., 67: 303-315, pls. 43, 44.
- LAWS, C. R., 1938, Ibidem. No. 5. The eullimellid genera. lb., 68: 51-59, pl. 9.
- LAWS, C. R., 1939, Ibidem. No. 6. The genus *Odostomia*. lb., 69: 191-209.
- LAWS, C. R., 1940, Ibidem. No. 7. Further odostomid genera. lb., 70: 150-160.
- LAWS, C. R., 1941, Ibidem. No. 8. The pyrgulinid genera. lb., 71: 6-22.
- LEBOUR, M., 1932, The eggs and early larvae of two commensal gastropods, *Stilifer stylifer* and *Odostomia eulimoides*. *Journal of the Marine Biological Association of the United Kingdom*, 18: 117-119.
- LINNAEUS, C., 1758, *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio Decima, Reformata. Tomus I, Holmiae: Laurentii Salvii, iv + 823 pp. [Reprinted, 1939, London: British Museum (Natural History)]
- LIPSCOMB, D., 1984, Methods of systematic analysis: the relative superiority of phylogenetic method. *Origin of Life*, 13: 235-248.
- LIPSCOMB, D., 1992, Parsimony, homology and the analysis of multistate characters. *Cladistics*, 8: 45-65.
- LIPSCOMB, D., 1993, *An introduction to cladistic methods: an overview of the basic procedures in phylogenetic systematics and use of the Hennig86 program*. In press.
- MAAS, D., 1963, Über Cuticularbildungen am Penis von Pyramidelliden. *Zoologischer Anzeiger*, 173: 137-148.
- MAAS, D., 1965, Anatomische und histologische Untersuchungen am Mundapparat der Pyramidelliden. *Zeitschrift für Morphologie und Ökologie der Tiere*, 54: 566-642.
- MACNAE, W. & M. KALK, 1958, *The fauna and flora of sand flats at Inhaca Island, Mocambique*. A natural history of Inhaca Island, Mozambique. Witwatersrand University Press, Johannesburg, 159 pp.
- MERRILL, A. & R. PETIT, 1965, Mollusks new to South Carolina. *The Nautilus*, 79: 58-66.
- MCFADDEN, Y. & A. MYERS, 1989, The life history and reproductive biology of *Odostomia eulimoides* (Gastropoda: Opisthobranchia) on the south coast of Ireland. *Journal of the Marine Biological Association of the United Kingdom*, 69: 65-80.
- MINICHEV, Y. S. & Y. I. STARBOGATOV, 1979, Peculiarities of the evolution of reproductive system of the Opisthobranchia and their taxonomy. Pp. 16-20, in: *Molluscs, Main Results of Their Study*. I. M. LIKHAREY ed. USSR Academy of Science Zoological Institute (Russian with English title; English version published Malacological Review, 17: 112-114).
- MOORE, D. M., 1966, The cyclostremellidae, a new family of prosobranch mollusks. *Bulletin of Marine Science*, 16: 480-484.
- MONTFORT, P. D. DE, 1810, *Conchyliologie systématique et classification méthodique des coquilles*. Paris, volume 2: 676 pp.
- MÖRCH, O. A. L., 1852, *Catalogus conchyliorum quae reliquit D. Alphonso d'Aguirra and Gadea Comes de Yoldi, regis daniae cubiculariorum princeps, ordinis dannebrogici in prima classe and ordinis caroli tertii eques*. Fasciculus primus Cephalophora. Hafniae, Typis Ludovici Kleini, 170 pp.
- MÖRCH, O. A. L., 1865, On the systematic value of the organs which have been employed as fundamental characters in the classification of Mollusca. *Annals and Magazine of Natural History*, (3)16: 385-397.
- MÖRCH, O. A. L., 1875, Synopsis Molluscorum marinarum Indiarum occidentalium. *Malakozologische Blätter*, 22: 142-184.
- MORRISON, J., 1939, Two new species of *Sayella* with notes on the genus. *The Nautilus*, 53: 43-45.
- NISHINO, T., S. NOJIMA & T. KIKUCHI, 1983, Quantitative studies life history and interspecific relationship of two gastropod species, *Odostomia* sp. (ectoparasite) and *Umbonium* (*Suchium*)

- moniliferum* (Lamarck) (host). I. Life history and population dynamics of *Odostomia* sp. *Publications Amakusa Marine Biological Laboratory, Kyushu University*, 7: 61–79.
- NOMURA, S., 1936, Pyramidellidae from Siogama Bay, Northeast Honsyū, Japan. *Saito Ho-on Kai Museum, Research Bulletin*, 10: 108 pp., pls. 1–22.
- NOMURA, S., 1937, Additional Pyramidellidae from Siogama Bay, with remarks on the molluscan fauna, especially Pyramidellidae from Sagami Bay; being a comparative study. *Saito Ho-on Kai Museum, Research Bulletin*, 12: 107 pp., pls. 1–14.
- NOMURA, S., 1938, The third report on Pyramidellidae based upon the specimens preserved in the collection of Saito Ho-on Kai Museum. *Saito Ho-on Kai Museum, Research Bulletin*, 16: 88 pp., pls., 1–15.
- NOMURA, S., 1939, *Summary of the fossil and recent Japanese Pyramidellidae, with the description of several new species. Saito Ho-on Kai Museum. Jubilee Publication in commemoration of Prof. H. Yabe's 60th birthday*, 119–156, pl. 9.
- NOMURA, S., 1940, Supplement of the fauna of the Japanese pyramidellid molluscs. *Saito Ho-on Kai Museum, Research Bulletin*, 19: 56 pp.
- NORDSIECK, F., 1972, *Die europäischen Meeresschnecken (Opisthobranchia mit Pyramidellidae; Rissoacea)*. Vom Eismeer bis Kapverden, Mittelmeer und Schwarzes Meer, Gustav Fischer Verlag, Stuttgart, i–xiii, 327 pp.
- ODÉ, H. & A. B. SPEERS, 1972, Notes concerning Texas beach shells. Superfamily Pyramidellacea. Part II. the odostomiid genera and the genus *Longchaeus*. *Texas Conchologist*, 9: 1–17.
- PELSENEER, P., 1899, Recherches morphologiques et phylogénétiques sur les mollusques archaïques. *Académie Royale des Sciences, des lettres, et des Beaux-Arts de Belgique, Mémoires Couronnés*, 57: 112 pp.
- PELSENEER, P., 1914, Ethologie de quelques *Odostomia* et d'un *Monstrillide* parasite de l'un d'eux. *Bulletin Scientifique de la France et de la Belgique*, 7: 1–21.
- PELSENEER, P., 1928, Les parasites des mollusques et les mollusques parasites. *Bulletin de la Société Zoologique de France*, 53: 158–189.
- PERRY, L. & J. SCHWENGLER, 1955, *Marine shells of the western coast of Florida*. Paleontological Research Institution, Ithaca, New York, 318 pp., pls. 1–55.
- PONDER, W. F., 1973, *Pseudoskenella depressa* gen. et. sp. nov., an ectoparasite on *Galeofaria*. *Malacological Review*, 6: 119–123.
- PONDER, W. F., 1987, The anatomy and relationships of the pyramidellacean limpet *Amathina tricarinata* (Mollusca: Gastropoda). *Asian Marine Biology*, 4: 1–34.
- PONDER, W. F., & A. WARÉN, 1988, Classification of the Caenogastropoda and Heterostropha—a list of the family-group names and higher taxa. In: *Prosobranch phylogeny*, W. F. PONDER, ed. *Malacological Review, Supplement*, 4: 288–346.
- POWELL, A., 1979, *New Zealand Mollusca. Marine, land and freshwater shells*. Collins; Auckland, Sydney & London. 500 pp.
- RASMUSSEN, E., 1944, Faunistic and biological notes on marine invertebrates I. The eggs and larvae of *Brachystomia rissoides* (Hanl.), *Eulimella nitidissima* (Mont.), *Retusa truncatula* (Brug.) and *Embletonia pallida* (Alder and Hancock), (Gastropoda marina). *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 107: 207–233.
- RASMUSSEN, E., 1951, Faunistic and biological notes on marine invertebrates II. The eggs and larvae of some Danish marine gastropods. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 113: 201–249.
- REHDER, H., 1935, New Caribbean marine shells. *The Nautilus*, 48: 127–130, pl. 7, figs. 7–12.
- REID, D. G., 1989, The comparative morphology, phylogeny, and evolution of the gastropod family Littorinidae. *Philosophical Transactions of the Royal Society of London, B-Biological Sciences*, 324: 1–110.
- REMANE, A., 1955, Morphologie als Homologienforschung. *Zoologischer Anzeiger, Suppl.* 18: 159–183.
- RISBEC, J., 1955, Considérations sur l'anatomie comparée et la classification des gastéropodes prosobranches. *Journal de Conchyliologie*, 95: 45–82.
- RISSO, A., 1826, *Historie naturelle des principales productions de l'Europe Méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes*, Vol. 4. F. G. Levrault, Paris, vii + 439 pp., pls. 1–12.
- ROBERTSON, R., 1957, Gastropod host of an *Odostomia*. *The Nautilus*, 70: 96–97.
- ROBERTSON, R., 1967, The life history of *Odostomia bisuturalis*, and *Odostomia* spermatophores (Gastropoda: Pyramidellidae). *Year Book of the American Philosophical Society*, 1966: 368–370.
- ROBERTSON, R., 1974, The biology of the Architectonicidae, gastropods combining prosobranch and opisthobranch traits. *Malacologia*, 14: 215–220.
- ROBERTSON, R., 1976, Marine prosobranch gastropods: larval studies and systematics. *Thalassia Jugoslavica*, 10: 213–238.
- ROBERTSON, R., 1978, Spermatophores of six eastern North American pyramidellid gastropods and their systematic significance (with the new genus *Boonea*). *Biological Bulletin*, 155: 360–382.
- ROBERTSON, R., 1985, Four characters and the higher category systematics of gastropods. *American Malacological Bulletin, Special Edition*, 1: 1–22.
- ROBERTSON, R. & V. ORR, 1961, Review of pyramidellid hosts, with notes on an *Odostomia* par-

- asitic on a chiton. *The Nautilus*, 74: 85–91, pls. 5, 6.
- ROBERTSON, R. & T. MAU-LASTOVICKA, 1979, The ectoparasitism of *Boonea* and *Fargoa* (Gastropoda: Pyramidellidae). *Biological Bulletin*, 157: 320–333.
- SALVINI-PLAWEN, L., 1980, A reconsideration of systematics in the Mollusca (phylogeny and higher classification). *Malacologia*, 19: 249–278.
- SCHELTEMA, A. H., 1965, Two gastropod hosts of the pyramidellid gastropod *Odostomia bisuturalis*. *The Nautilus*, 79: 7–10.
- SCHOCH, R. M., 1986, *Phylogeny reconstruction in paleontology*. Van Nostrand Reinhold, New York, 351 pp.
- SCHUH, R. T. & J. S. FARRIS, 1981, Methods for investigating taxonomic congruence and their applications to the Leptocomorpha. *Systematic Zoology*, 30: 331–351.
- SHEEHAN, D. C. & B. B. HRAPCHAK, 1980, *The theory and practice of histotechnology*, 2nd ed. C. V. Mosby Company, St. Louis, 481 pp.
- SOWERBY, G. B., II, 1865–1870, *Conchologia Iconica: or, Illustrations of the shells of molluscos animals*. In: L. A. REEVE. Sowerby, London, volumes 15–18, 337 pp.
- STIMPSON, W., 1851, Notices of several species of testaceous mollusca new to Massachusetts Bay. *Proceedings of the Boston Society of Natural History*, 4: 12–18.
- TAYLOR, D. W. & N. F. SOHL, 1962, An outline of gastropod classification. *Malacologia*, 1: 7–32.
- THIELE, J., 1929–35, *Handbuch der systematischen Weichtierkunde*. Jena, Gustave Fischer, 1154 pp.
- THOMPSON, T. E., 1976, *Biology of opisthobranch molluscs*. Volume I. London, Ray Society, pp. 206.
- THORSON, G., 1946, Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planctonic larvae of the Sound (Oresound). *Meddelelser fra Kommissionen for Danmarks Fiskeri og Havundersogelser*, Serie Plancton, 4: 1–523.
- THORSON, G., 1950, Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews*, 25: 1–45.
- TRYON, G. W., Jr., 1886, *Manual of conchology, structural and systematic*. Volume 8. Naticidae, Calyptraeidae, Turritellidae, Vermetidae, Caecidae, Eulimidae, Turbonillidae, Pyramidellidae. Privately published, Philadelphia, 461 pp., pls 1–79.
- TUOMEY, M. & F. S. HOLMES, 1855–57, *Pleiocene fossils of South Carolina: containing descriptions and figures of the Polyparia, Echinodermata and Mollusca*. Russell Jones, Charleston, South Carolina, xvi + 152 pp., 30 pls.
- USTISKE, G. W. NOWELL, 1959, *A check list of the marine shells of St. Croix U.S. Virgin Islands with random annotations*. Lane Press, Burlington, Vermont, 90 pp.
- USTISKE, G. W. NOWELL, 1969, *A supplementary listing of new shells (illustrated) to be added to the check list of the marine shells of St. Croix*. Privately published, 32 pp.
- USTICKE, G. W. NOWELL, 1971, *A supplementary listing of new shells (illustrated) revised edition to be added to the check list of the marine shells of St. Croix*. Privately published, 32 pp.
- VAN DER LINDEN, J. & J. C. A. EIKENBOOM, 1992, On the taxonomy of the Recent species of the genus *Chrysalida* Carpenter from Europe, the Canary Islands and the Azores (Gastropoda, Pyramidellidae). *Basteria*, 56: 3–63.
- VERRILL, A. E. & K. BUSH, 1900, Additions to the marine mollusca of Bermudas. *Transactions of the Connecticut Academy Sciences*, 10: 513–544.
- WATROUS, L. E. & Q. D. WHEELER, 1981, The outgroup method of character analysis. *Systematic Zoology*, 30: 1–11.
- WELLS, H., 1959, Notes on *Odostomia impressa* (Say). *The Nautilus*, 72: 140–144.
- WELLS, H. J. & M. J. WELLS, 1961, Three species of *Odostomia* from North Carolina, with description of new species. *The Nautilus*, 74: 149–157.
- WENZ, W., 1938–44, Gastropoda. Teil 1. Allgemeiner Teil und Prosobranchia. In: *Handbuch der Paläozoologie*, Vol. 6, O.H. SCHINDEWOLF, ed. Berlin, Brontraeger, 1639 pp.
- WHITE, M., C. KITTING & E. POWELL, 1985, Aspects of reproduction, larval development, and morphometrics in the pyramidellid *Boonea impressa* (= *Odostomia impressa*) (Gastropoda: Opisthobranchia). *The Veliger*, 28: 37–51.
- WINCKWORTH, R., 1943, Holten's systematic list of the shells of Chemnitz. *Proceedings of the Malacological Society of London*, 25: 146–150, pl. 5.
- WISE, J. B., 1993, Anatomy and functional morphology of the feeding structures of the ectoparasitic gastropod *Boonea impressa* (Pyramidellidae). *Malacologia*, 35: 119–134.